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MORPHOLOGY OF RUMEX CRISPUS

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(WITH PLATES XVII–XIX AND TWENTY-ONE FIGURES)

Introduction

A chance examination of a stem of *Rumex crispus* L. showed the presence of well developed internal bundles. Since this character is to be regarded as advanced, Dr. W. J. G. LAND suggested that it might be of interest to investigate the morphology of the entire plant. This paper is concerned only with an account of the morphology of the floral structures; a study of the vascular situation is already under way.

Aside from monographs, the genus *Rumex*, and indeed the entire family Polygonaceae and order Polygonales, have received little attention. FINK (3) made a study of the ovular structures in *R. verticillatus* L. and *R. mexicanus* Meisn. (*R. salicifolius* Man.), which develop very similarly. The archesporial cell cuts off a primary wall cell, then forms a linear tetrad, the innermost megaspore of which functions. He found approximately 24 chromosomes in the spindle of the first division of the megaspore mother cell, but was not certain whether this was a true reduction division. A regular 8-nucleate embryo sac is formed, and pollen tubes enter, although actual fusion of the gametes was observed but once, and that in an unfavorable preparation. ROTH (8) investigated several European

species of *Rumex*, among them *R. crispus*. He found the haploid number of chromosomes in the microspore mother cells to be 8 in *R. Acetosa, R. hispanica, R. arifolius,* and *R. nivalis;* 16 in *R. Acetosella;* and probably 40 in *R. cordifolius*. *R. Acetosa* apparently undergoes reduction in the megaspore mother cell, although he saw no indication of subsequent fertilization. The embryo sac very frequently degenerates. He found evidence of apogamy in some species, and thinks it probable that, at least in the group *Acetosa*, this has been the result of dioecism. STRASBURGER (9) early investigated *Polygonum divaricatum*, and his figures of the origin and development of the embryo sac have become a classic example of normal behavior.

Material and methods

Inflorescences and individual flowers of various ages were collected along street borders near the University of Chicago, and in a flood plain pasture near Mineral Springs, Indiana, during the summers of 1915 and 1916. They were killed in chrom-acetic, imbedded in paraffin, and cut in the usual manner. Both iron alum-hematoxylin and safranin-gentian violet were employed for staining.

Some of the most important features of the morphology became apparent in the course of the investigation during the winter of 1916–17, and as no more material could be obtained then, there remain some points the solution of which requires the collection of more flowers and careful observations on the growing plants.

Normal development

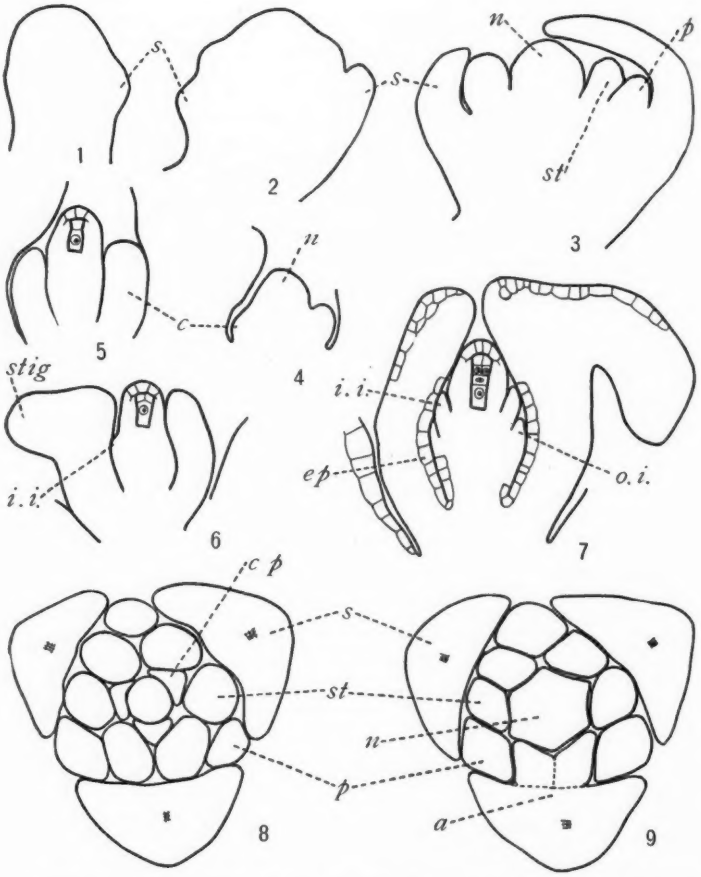
ORGANOGENY.—The young inflorescence of *Rumex crispus* is closely invested by the sheaths of successive bracts. It is profusely branched, and the branches bear flower buds of considerable size before they emerge from the protecting sheaths. All the young parts are covered with a mucilaginous secretion, rendering the penetration of reagents slow.

The flowers are borne in clusters at the nodes. The oldest are nearest the main stem, while the successively younger arise outside these, on the upper surface of the enlarged projecting nodes.

The sequence of development of the floral organs is centripetal, although the petals and carpels are somewhat delayed (figs. 1–7). The sepals appear as 3 thick prominences, and rapidly grow up over the young flower. The 3 petals appear almost simultaneously with the stamens, which they closely resemble at first (figs. 3, 8, 9). The 6 stamens appear in pairs, the 2 of each pair arising so close together that their bases are joined to each other and to the sepal opposite which they lie (fig. 9*a*). The carpels first appear as a thick ring about the base of the nucellus, but the latter develops much more rapidly and is not inclosed by them until the megaspore mother cell is considerably enlarged (figs. 4–7). The carpels develop as a continuous ring led by 3 growing points (fig. 8), until the ovarial cavity is inclosed, when the 3 points continue separately to form the styles and stigmas (figs. 6, 7). The styles are reflexed so that the much branched stigmas are finally placed between the bases of the anthers.

The inner integument appears during the prophase of the first reduction division (fig. 6), and the outer appears with the homoiotypic division (fig. 7). Both are 2-layered from the beginning. The inner grows up beyond the nucellus, and turns inward to close up and form the micropyle. The outer integument never extends much beyond the tip of the nucellus. During the development of the embryo sac, the cells of the outer layer of the outer integument and the epidermis of the ovary thicken, lose their contents, and form a continuous impervious layer (fig. 7; see also figs. 13, 14). This process is significant, because it leaves only the chalazal region of the ovule as a point of intake for nutrient materials.

MEGASPOROGENESIS.—The terminal cell of a definite axial row in the nucellus enlarges as the archespore (fig. 22). It soon divides to form the primary parietal cell and the megaspore mother cell (fig. 23). The parietal cell divides twice by anticlinal walls to form a cap of 4 cells (figs. 24, 28). Occasionally any or all of these cells may divide by a periclinal wall (figs. 25, 32). Less frequently, a cell or two of the adjacent epidermis may also divide periclinally (figs. 33, 36, 44). Occasionally there are two archesporial cells, and in one ovule there was a mass of probably 7 archesporial cells, a few of which had undergone the first division. In the most



FIGS. 1–9.—Organogeny: fig. 1, appearance of sepals (*s*); figs. 2, 3, simultaneous appearance of petals (*p*) and stamens (*st*), nucellus (*n*); figs. 4, 5, early development of carpels (*c*); fig. 6, appearance of inner integument (*ii*) and beginning of stigma (*stig*); fig. 7, appearance of outer integument (*oi*) and early thickening of epidermal cells (*ep*) over outside of ovule and walls of ovary; figs. 8, 9, transverse sections of same flower, showing relation of parts, growing points of carpels (*cp*), and union of stamens to each other and to sepal (*a*); figs. 1–7, ×175; figs. 8, 9, ×155.

advanced case observed, the 2 megaspore mother cells had fully enlarged and were in prophase of the heterotypic mitosis (fig. 24). They were separated by a crushed cell of equal length, which may have been a megaspore mother cell, but more probably was only a vegetative cell that became so crushed that it could not divide, and was forced to elongate with the enlarging mother cells.

The megaspore mother cell enlarges and elongates considerably, then undergoes two successive divisions to form a tetrad of cells (fig. 28). Apparently this division is a true reduction, for all the stages seem to be normal, and at diakinesis there are 32 pairs of chromosomes (fig. 26). While an accurate count of the chromosomes could not be made on the spindle, careful estimation indicates that the number still is 32 (fig. 27). In the vegetative cells the spindle is shorter, and proportionally much broader, and while the chromosomes are too small and too densely massed to be definitely counted at any stage, they clearly are more numerous than in the megaspore mother cell; I could only estimate that there are about twice as many, that is, 64.

Wall formation follows each of the reduction mitoses. The first wall usually divides the mother cell a little above the center (fig. 30). The second wall is usually near the outer end of the inner cell (figs. 29, 30), although in the best preparation found (fig. 28) the cell is nearly equally divided. The wall in the outer cell is always longitudinal, instead of transverse (fig. 28). There is some irregularity in the sequence of the homoiotypic division; usually the inner cell divides first (fig. 30); sometimes the divisions are simultaneous (fig. 28); and in one case the outer cell was the first to divide.

The inner megaspore functions, and the others quickly degenerate (fig. 29). The third megaspore rarely forms a normal cell, and is usually the first to degenerate (figs. 31, 33). The outer cell may degenerate before it has a chance to divide, or the 2 megaspores may degenerate before they are separated by a wall (fig. 31).

Embryo sac.—The functioning megaspore rapidly elongates and develops a large vacuole at each end, with the nucleus centrally placed (figs. 33–35). The daughter nuclei migrate to the poles, where two more mitoses produce 8 nuclei (figs. 38, 42, 44). The

mature sac is of the usual organization (fig. 46). The outer end enlarges greatly, crushing the parietal and adjacent nucellar cells, and comes to lie in contact with the epidermis of the nucellus. The extreme inner end remains small through this and subsequent development, and in it the 3 antipodal cells are cut off by walls. While they persist until the embryo is of considerable size, they never manifest any activity (fig. 47). The polar nuclei fuse early (figs. 44–47), and the fusion nucleus lies well toward the outer end of the sac. The egg apparatus is typical.

DEVELOPMENT OF STAMENS.—The stamen primordia are at first oval in cross-section (fig. 8), but early differentiation of the archesporial cells makes them somewhat rectangular, and sets off the anther region from the filament. The archespores are single rows of cells (fig. 48); each soon divides by a periclinal wall to form the primary parietal cell and the primary microsporogenous cell (fig. 49), then both divide anticlinally. Frequently the anticlinal division precedes the periclinal (fig. 50). There are 2 periclinal divisions in the primary parietal cell, and an appropriate number of transverse divisions to keep pace with the rapidly elongating anther. The first (fig. 54) sets off a layer that finally differentiates into a well marked endothecium with characteristic spiral thickenings; the second (fig. 57) forms the middle wall layer and the tapetum, and takes place about the same time as the last division in the sporogenous tissue. The middle layer is soon crushed and obliterated (fig. 58).

The tapetal cells appear to behave in all possible ways. According to BONNETT (1) the nucleus usually divides twice by normal mitoses, after which there may occur a great variety of nuclear fusions and abnormal mitoses. In some cases there is but one division. Usually in *Rumex crispus* the tapetum becomes binucleate; often it is multinucleate; and now and then there may appear large irregular nuclei with many nucleoli, as if formed by the fusion of a number of small nuclei (fig. 61). Apparently the normal condition is for the tapetum to persist as a functioning nutritive layer up to the liberation of the microspores from the tetrad (fig. 63); but in keeping with the widespread degenerations occurring throughout the flower, it may begin to degenerate while

the microspore mother cells are entering reduction (fig. 58). The cytoplasm becomes vacuolate, the nucleus stains very deeply, and shortly the entire protoplast collapses.

Before the microspore mother cell stage, the epidermis over most of the anther begins to enlarge and thicken, and the protoplasts to disorganize. This thickening extends to the cells of the connective, so that each loculus becomes inclosed by an impervious layer, except in the stomial region (fig. 10). Here a plate of the

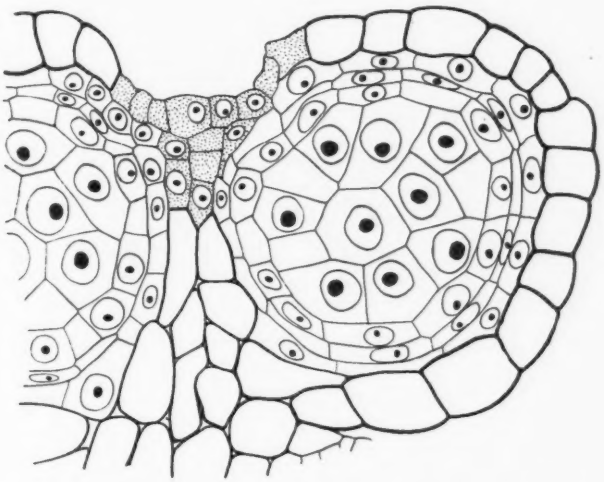


FIG. 10.—Portion of transverse section of fully differentiated anther, showing thickened epidermis continuous with thickened connective, and permanently juvenile tissue (shaded), subsequent disorganization of which first connects the two adjacent loculi, then dehisces the resulting pollen chamber; ×730.

epidermis a few cells wide, together with the outer half of the tissue between adjacent loculi, remains undifferentiated, as a special mechanism for dehiscence. As the anther matures, these weak cells break down, first joining the cavities of the adjoining loculi to form the pollen chamber, then opening this chamber to the exterior.

MICROSPOROGENESIS.—The primary sporogenous cells undergo three or four successive divisions to form the completed sporogenous tissue. At the same time the anther has elongated greatly,

so that in each loculus there come to be 9–12 mother cells in transverse section, and 15–20 in longitudinal section (fig. 57). Just before reduction there is conspicuous enlargement of the anther, stretching the walls of the mother cells, and allowing the protoplasts to round off. The cytoplasm of the mother cells is rather dense and finely granular, and the nuclei are large with scanty chromatin.

Reduction appears to be normal. No attempt was made to trace the details. At diakinesis there are 32 pairs of chromosomes (fig. 60), as found in the megaspore mother cells. The formation of a tetrahedral tetrad, the development of a thick cellulose wall about it, wall formation about the microspores, and liberation of the microspores from the tetrad by disorganization of the thick common wall, all follow the usual procedure for dicotyledons. At first rather dense, the cytoplasm of the microspores does not keep pace with the enlargement of the cell, and becomes rather finely vacuolate (fig. 64). It is not certain whether this is entirely normal; indeed, degeneration is so universal that it is difficult to determine whether there is such a thing as normal development of the microspore.

The nucleus of the microspore divides into tube and generative nuclei, and the latter organizes a small cell about itself (figs. 67, 68). Before shedding, the generative cell produces two male nuclei (figs. 71, 72); very few pollen grains ever reach this stage with anything approaching what may be considered normal appearance. The exine becomes well thickened and delicately rugose. Three germ pores are formed, beneath which the intine is slightly thickened (figs. 65, 66); they are connected with each other by furrows over the surface.

FERTILIZATION.—Any conclusion for or against fertilization must for the present depend entirely on negative evidence. Some of the facts observed point rather conclusively to the occurrence of fertilization. There is no doubt that there is diakinesis in the megaspore mother cell, that there are 32 diads, and that this is the number present in the microspore mother cells also. While the exact number of chromosomes on the spindle of the heterotypic mitosis could not be counted, it appears to be 32 (fig. 27); the achromatic figure has all the characteristics of a reduction spindle; and finally a

tetrad of cells results. Further, the polar nuclei fuse early, a process characteristic of normal haploid embryo sacs; and a fair number of embryos is formed. Many embryo sacs have the appearance of having waited a long time for fertilization, before finally degenerating (fig. 47). On the other hand, there is equally convincing evidence that fertilization does not occur. I cannot be sure that I have seen normal pollen in any instance; that which might be considered normal is so scarce that there seems little chance for adequate pollination. Some pollen grains have been observed on the stigmas, but they all had the appearance that is believed to indicate degeneration, and certainly none of them was germinating. At the same time, the stigmas wither early, and most of them would seem to be incapable of supporting pollen tube growth. No pollen tubes were ever observed, either in the styles or in the micropyles, nor any densely staining remains that might indicate the position of former tubes. The dead impervious layer over the outer integument would seem to preclude the entrance of pollen tubes through any other point than the micropyle and the tip of the nucellus. No fusion of gametes, which after all is the final proof of fertilization, was seen; indeed, in all the preparations I have made and examined I have seen just one embryo sac that contained a normal appearing egg apparatus (fig. 46), and it was in a still unopened flower. In the many flowers I have examined in section, only a relatively small number contained embryos.

It is possible that *Rumex crispus* behaves as OVERTON (7) found for *Thalictrum purpurascens*, where some megaspore mother cells undergo normal reduction, producing haploid embryo sacs and reduced eggs that require fertilization for further development, while other megaspore mother cells fail to reduce, and give rise to diploid sacs and eggs, the latter developing embryos apogamously. If this should prove to be the situation in *Rumex crispus*, then it would be expected that the embryos arise apogamously from unreduced eggs. I regret that there has been no opportunity to collect new material to settle this important question.

SUBSEQUENT DEVELOPMENT OF FLOWER.—It is beside the purpose of this paper to discuss the details of fruit development, and

only the early stages have been investigated. As previously mentioned, only a relatively small number of flowers ever proceed to fruit formation. The embryo and endosperm are of the well known *Capsella* type; the suspensor may become about 10 cells long, and occasionally some of the cells divide longitudinally. All parts of the ovule elongate greatly, and the integuments and walls of the nucellus finally become compacted into a single thin layer. The carpels become much thickened and the cells strongly lignified. The petals enlarge and elongate to keep pace with the developing fruit, and function as protective organs (valves), while the tissue on the abaxial side of the midrib of each proliferates and forms the characteristic tubercles. The sepals alone, of all the structures in the maturing flower, fail to enlarge, and remain tiny flaps at the bases of the petals.

Degenerations

It soon became apparent that the most striking and significant feature in the flowers of *Rumex crispus* is the wholesale degenerations that occur. These degenerations may go on in either the stamens or the carpels, or in both at the same time. They are characterized in some cases by lighter staining and increasing vacuolation of the cytoplasm, until it becomes an almost indistinguishably thin peripheral layer, and the aggregation of the chromatin into fewer and larger masses, with irregular outline of and final collapse and disintegration of the nucleus. Such changes are characteristic in the earlier stages of development of the stamens. In other cases, the cytoplasm increases in density and staining power, and plasmolyzes away from the walls; the nucleus becomes deeply and uniformly granular, and finally stains as a solid homogeneous mass; the protoplast ultimately shrinks into a blob in which no trace of the original structure can be distinguished.

DEGENERATIONS IN THE STAMENS.—Degenerations in the stamens may begin at any stage, from the primary sporogenous cell to the pollen grain, and may involve part or all of the sporogenous tissue, part or all of the microspore mother cells, one to all of the spores of a tetrad, any or all of the microspores, and any or all of the pollen grains, in any or all of the loculi of the anthers, in

any or all of the flowers of an inflorescence, and may or may not be accompanied by disorganization of the corresponding parts of the anthers. No instance has been observed of failure of all 6 anthers to start normal development, and nothing indicating disturbances in this development appears in the archesporial cell stage. It is very common, however, for the primary sporogenous cells to acquire small vacuoles (fig. 50), which merge into larger and larger vacuoles (fig. 51), until finally the cytoplasm is only a thin membrane lining the walls of the cell. It stains less and less intensely as the process goes on. The chromatin becomes aggregated into fewer and larger masses, which lie closely appressed to the nuclear membrane, and which stain very deeply. The nucleolus soon becomes indistinguishable. The nucleus becomes irregular in outline and shrinks, and in turn almost disappears. At the same time, the primary parietal cell, connective cells, and surrounding epidermis undergo a similar disorganization. Such a process usually is not confined to a single loculus, or even to a single anther, but includes all the stamens of a flower. Apparently if the degeneration process is not intense such cells may continue dividing for a time, forming anthers with all parts in normal relation (figs. 55, 56). Finally the cells become too weakened to divide further, and are nearly or quite empty. Anthers may be found in this condition that have developed almost to the mother cell stage. In the end, the arrested stamens break down and disappear completely before the flower opens.

In other flowers the anthers may start normally, but individual cells in the sporogenous mass begin to degenerate, while the others, at least for a time, appear to continue normally (figs. 53, 54). Both cytoplasm and nucleus become more coarsely granular and very dense, and stain intensely. The protoplast pulls away from the cell walls, finally becoming only a shapeless dense mass in the central part of the cell. This process involves all the loculi of all the anthers of a flower, and may occur at any stage up to and including the mother cells.

Normal microspore mother cells round off evenly and uniformly when the anther enlarges, and stain moderately. Mother cells in the process of degeneration round off into irregular masses, and

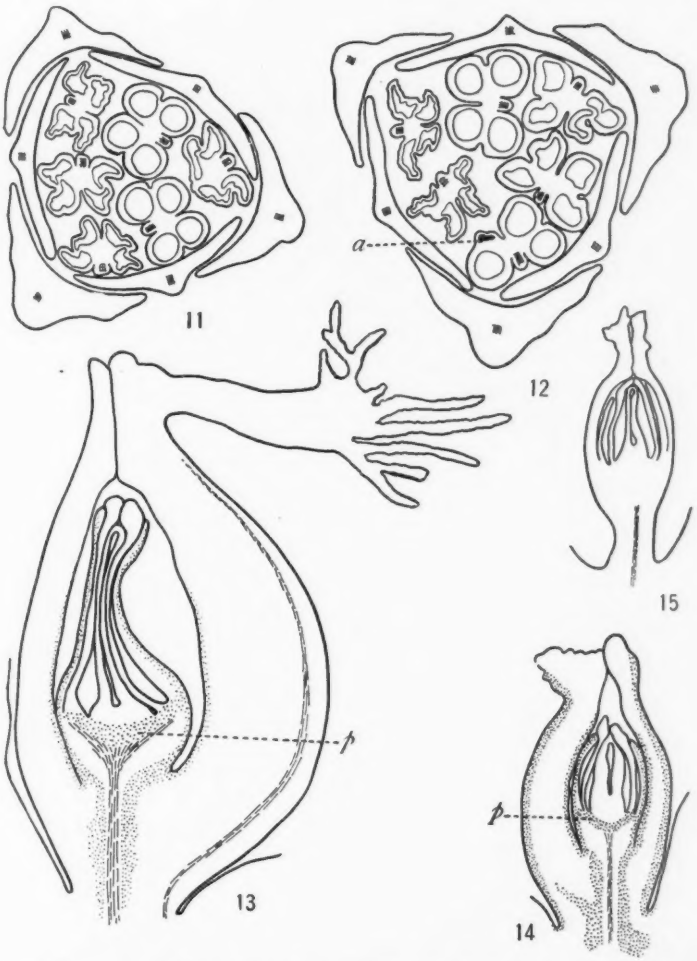
stain more or less intensely according to the degree of disorganization. These cells are capable of passing through the reduction divisions (fig. 61), and chromosome number, spindles, and the tetrads formed appear to be normal in essential features, but they stain very deeply and the outlines are irregular.

Usually if the anther walls have developed unimpaired to the reduction stage, they can reach maturity and produce a normal appearing organ. Many, however, begin to collapse, and it is very common to find examples in which the walls have collapsed closely against the sporogenous tissue within, while the cells and walls are much wrinkled and distorted (fig. 61). Earlier degenerations are likely to include all the stamens of a flower; later degenerations may include only one or two loculi of one anther, or only one or a few of the 6 anthers (figs. 11, 12). In one case in particular, one of the loculi of an anther had degenerated early and left only a small deeply staining spot at the side of an otherwise normal organ (fig. 12*a*).

As already mentioned, the tapetum is involved along with the other parts. A few anthers have been observed in which the sporogenous cells had degenerated completely into dense shapeless masses, while the walls and tapetum had remained relatively unaffected; the wall cells were thicker than normal, and the tapetal cells had become much larger and projected like papillae against the contracted, disorganized, sporogenous tissue (fig. 59).

By the time reduction is completed, the tendency to degeneration has become so universal that only a few microspores appear normal. It is not uncommon to find even the spores of a tetrad in widely different stages of disorganization; one or two will appear almost normal, while the others are mere masses of stain (fig. 62). In such cases it is certain that spores that do not stain so intensely are really affected. Spores that survive liberation from the tetrad may shrivel up, with the cytoplasm more and more closely packed about the diminishing nucleus, until finally nothing is left but the wall with a little mass collapsed against one side (figs. 63, 65, 66).

Very many spores proceed to wall formation and the usual divisions to complete the male gametophyte. Only in a few



FIGS. 11–15.—Various degrees of degeneration in flower: figs. 11, 12, transverse sections of flowers at tetrad stage of microspores, showing indiscriminate failure of anthers; at *a*, fig. 12, a loculus disorganized early, while other three are developing normally; fig. 13, ovary well developed, ovule just beginning to collapse, and embryo sac with small amount of completely disorganized endosperm; fig. 14, both embryo sac and ovule disorganized; fig. 15, ovary in which degeneration began so early that nothing remains but dried remnants; shaded parts in figs. 13, 14 indicate thickened impervious cells, particularly chalazal plate (*p*); ending of ovular vascular bundle also shown; figs. 11, 12, ×50; figs. 13–15, ×155.

instances, however, do the cells produced look as if they might be normal. The cytoplasm is much vacuolated, and the nuclei are not distinct, even in the best of preparations (figs. 67, 68, 72, 73).

HYPERTROPHY OF POLLEN GRAIN.—Those grains that appear most nearly normal have little or no starch (fig. 67). Pollen grains that have proceeded to full wall development and generative cell formation begin to enlarge until about twice normal volume (fig. 68). In all such there is considerable accumulation of starch grains, and in some the cell is tightly packed with relatively enormous grains (fig. 69). Whenever the nuclei show at all, they are irregular in outline, poorly defined, and almost uniform in texture. Later, the starch is dissolved, and the contents of the pollen grain become more and more homogeneous, until in the end the grain is filled with a granular substance staining deeply and uniformly throughout. In the best preparations, some of these cells still showed the remains of the nuclei; but there is little doubt that they are destined to go to pieces (figs. 70–73). In every case the tube nucleus was irregular and difficult to trace, but often the two male nuclei, although very small, still held their shape and showed separate chromatin masses. Usually, however, only deeply and characteristically staining masses indicate the remains of the nuclei (figs. 71, 72, 75).

"POLLEN TUBE" FORMATION.—Hypertrophy of the pollen grains may be due to high osmotic pressure set up in the disintegrating contents. The starch formation undoubtedly is pathological. The conditions in the cell that induce starch formation probably also cause other changes, which lead to greatly increased osmotic pressure, which is further increased by the solution of the starch. Very frequently these large pollen grains put out pollen tubes through all three of the germ pores. These tubes may remain mere bulbs (fig. 72), or they may become many times the length of the cell producing them, and are always almost solidly filled with the dense homogeneous contents of the mother cell (figs. 74, 75). Often the disorganizing nuclei migrate into the tubes, and the pollen grain may be almost entirely emptied (fig. 74). The tubes often become inflated at the end, as if under pressure, and it appears that they sometimes burst.

The explanation of these tubes seems to be that the high osmotic pressure set up in the pollen grain literally blows the distensible intine out through the germ pores, and continues elongation of the tube as long as the pressure is maintained. Presently the pressure goes down and the process ceases. It may be that the retention of some semblance of organization by the nuclei indicates that the cell is not dead, and that tube formation is a weak abnormal growth process. Finally, the contents of the grain begin to shrivel (fig. 74), the walls become wrinkled and collapse, and the cell dries up. By the time the anthers open, little or no trace of the pollen tubes remains, and the nuclear material is no longer distinguishable. I would estimate that 99 per cent of the pollen grains undergo some such degeneration process. Very infrequently one can find a grain of normal size with the nuclei clearly outlined, lying among the hypertrophied grains, and occasionally one or two of the loculi of an anther will contain seemingly normal grains, while the remaining loculi are filled with the large cytolyzed grains.

Fungus invasions.—Such a mass of disorganizing cells would seem to be particularly favorable material for the growth of saprophytes. In every dehisced anther sectioned there was an abundant growth of an unidentified fungus. The septate hyphae ramify everywhere through the pollen chambers among the pollen grains, and in a very few instances were seen penetrating pollen grains through the germ pores (fig. 70), but with the appearance of a chance entrance, rather than a definite exploitation of the contents of the grains. It may be stated confidently that the fungus does not attack unopened anthers, for it never was present until after the anthers had opened. In those anthers where the fungus had been developing longest and had formed a felt of hyphae, it had produced a great abundance of minute spores.

Degenerations in ovary.—Degenerations just as widespread and devastating occur in the ovary also. They do not begin so early as in the anthers, never having been observed with certainty before reduction is completed (figs. 31, 32), although there are faint suggestions that even during the second reduction division the cells may not be entirely healthy. The non-functioning megaspores seem to degenerate prematurely, although this is by no

means an unusual feature in angiosperms. With the beginning of enlargement of the functioning megaspore the degeneration process becomes apparent (figs. 31, 32). It is always characterized by increasing density of both cytoplasm and nucleus, plasmolysis of the cytoplasm, and final collapse into a distorted strand in the center of the cell (figs. 36, 37). The disturbance occurs with increasing frequency through the various stages of embryo sac formation, 2- (figs. 39, 40, 41), 4- (fig. 43), and 8-nucleate (fig. 45) stages being found in more or less advanced degeneration, until by the time the sac should be mature, scarcely one remains untouched. In all the sections made and examined, I have seen just one normal appearing embryo sac. It is not a case of having overlooked the stage, for repeatedly late buds and open flowers showed the remains of sacs in all stages of disorganization (fig. 47).

At first, and in early embryo sac stages, only the sac itself is involved, but later the entire ovule becomes shriveled, with the individual cells deeply staining. If the process has begun early enough, it involves the entire ovary also. An open flower, therefore, may show all parts of the ovary normal except the embryo sac (fig. 13), or both embryo sac and ovule may be degenerating (fig. 14), or the entire ovary may be shriveled up, brown, and dead, a mere husk projecting up from the base of the flower (fig. 15).

Degenerations do not halt here, but may attack those ovaries in which embryo formation has begun. At any stage in the development of the fruit the ovule may collapse about the embryo and endosperm, which then take on the characteristic dense, deeply staining appearance. The ovary itself appears sometimes to continue normal development, at least for a time, or it may follow the other parts in degeneration. Certainly not more than 10 per cent of the flowers examined in section contained embryos, and of these not more than 10 per cent had the appearance of being able to reach maturity in a normal manner.

It is very striking that in every case a plate of dense impervious cells, several layers thick, was formed across the chalaza, connecting at the edges with the impervious layer over the outer integument and the ovary walls. Other and irregular patches of similar tissue appear in the funiculus, often seeming to involve

even the cells of the ovular vascular bundle (figs. 13, 14, 20). This bundle flares out against the lower side of the impervious chalazal plate (fig. 13), and there is no passage of normal cells anywhere connecting it with the nucellus. The lower end of the bundle terminates blindly in a patch of permanently thin-walled parenchyma, with absolutely no connection with the vascular system traversing the peduncle and branching to supply the other parts of the flower (figs. 19–21). Below this parenchyma, between the traces to the sepals and petals, and removed by 8–10 parenchyma cells from the end of the ovular bundle, the bundle of the peduncle terminates in a broad axial mass of short tracheids. One thinks of the patch of parenchyma as a reservoir, filled from the bottom by the bundles of the peduncle, and emptied by an ovular bundle dipping into the top.

DEGENERATIONS IN ENTIRE INFLORESCENCE.—Degenerations are not always confined to scattered flowers, but may involve all the flowers, especially the terminal portions of large or late inflorescences. The earlier in the development of the inflorescence that the degeneration processes set in, the larger is the number of flowers involved.

ABSCISSIONS.—Accompanying these degenerations is a strong tendency for parts to absciss. There is a definite abscission layer formed near the base of the peduncle (fig. 16), which leads to dropping off of those flowers in which extreme early degenerations have appeared. A ring of epidermis remains thin, and the underlying cortical cells remain meristematic. The exact method of operation has not been followed; it is probable that the mechanism is called into activity by the same causes that result in failure of the other floral parts.

The fully developed filament of the stamen is a short thick stalk, traversed by a small vascular bundle. All the mature stamens that were observed were either entirely separated from the flower, or at least physiologically separated, by disorganization of the upper end of the filaments. The epidermis and cortical cells break down, leaving the anther attached by the vascular bundle only (fig. 19*a*). Soon this is severed also, and the anther is held in the flower only by the floral envelop, to be dropped out upon

blooming. The stump of the filament continues disorganizing until finally only frayed out, dried remnants remain at the point of insertion.

RESULTS OF DEGENERATIONS.—Where degenerations involve both stamens and ovary at an early age, the entire bud drops before opening. A large percentage of the flowers of an inflores-

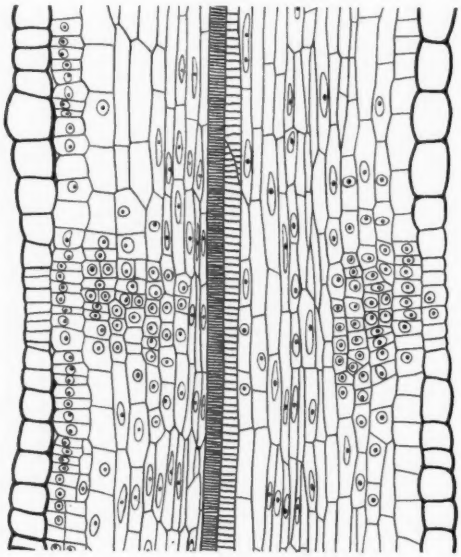
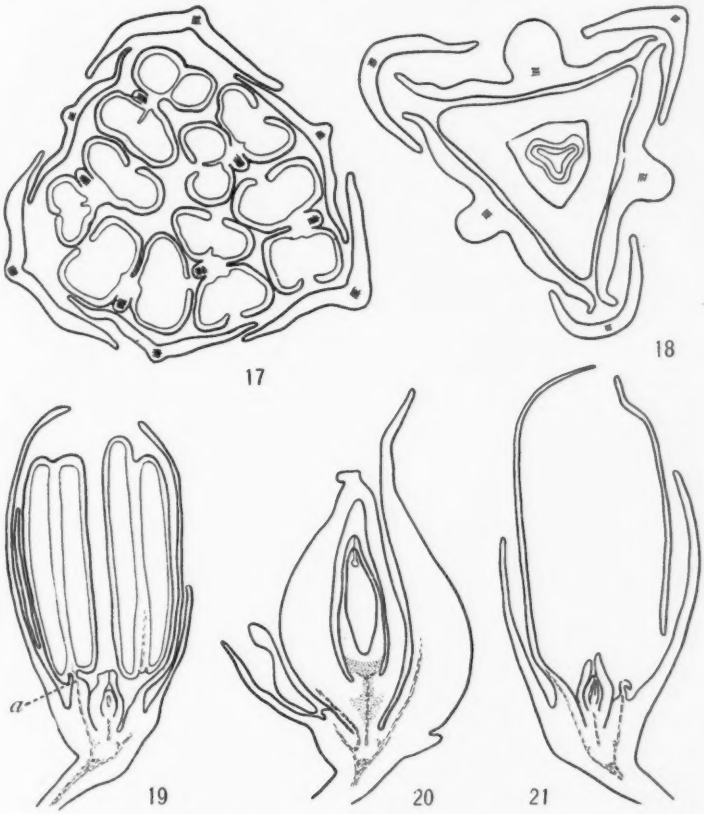


FIG. 16.—Longitudinal section through abscission region of peduncle; cells of epidermis are strongly thickened, and those of cortex are for the most part differentiated beyond point of further division, except in definite abscission zone, where divisions are still in progress; note large number of recently divided cells in subepidermal layer on left side; their subsequent elongation will produce the strong curvature of peduncle; ×350.

cence is lost in this way. Where the degenerations involve only the stamens or only the carpels, or when beginning later in the development of the flower, 4 distinct types of mature flowers are produced, with all gradations between.

1. Functional staminate flowers, in which any number of stamens, from one to all, reach maturity, although their products

usually are not functional. The ovary usually is well developed, but the embryo sac is sterile by degeneration. The sepals and petals are about equally developed; they have performed their function in protecting the essential organs in the bud, and make no



FIGS. 17–21.—Types of mature flowers: fig. 17, transverse section, and fig. 19, longitudinal section of a functional staminate flower; ovary is present but sterile by degeneration; anther on left in fig. 19 nearly severed by disorganization of filament at *a;* fig. 18, transverse section, and fig. 20, longitudinal section of functional ovulate flower at early stage of embryo development; stamens degenerated and disappeared before flower opened; fig. 21, longitudinal section of a sterile flower; stamens obliterated and ovule sterile by degenerations; figs. 17, 18, ×30; figs. 19–21, ×18.

further growth. The flowers have accomplished their purpose with the development of pollen, defective though that may be, and soon wither (figs. 17, 19).

2. Functional ovulate flowers, from which all the stamens have been eliminated by degeneration before the opening of the flower. In such flowers the stamens frequently disappear so early that the points of insertion are no longer discernible, and even the vascular traces have almost disappeared. An embryo begins to develop, and endosperm formation starts, although subsequently degeneration may overtake it, resulting either in death of the entire flower, or in development of a pseudo-parthenocarpic fruit. The sepals remain small, but the petals enlarge as protective organs and develop the characteristic tubercles (figs. 18, 20).

3. Bisporangiate flowers, containing both functional ovary and functional stamens. They are very rare; I have sectioned two such, and these had only one or two stamens each.

4. Completely sterile flowers, where degenerations have occurred in both stamens and carpels early enough to cause complete elimination of the former, but not severe enough to cause the flower to drop before blooming. The ovary may be in any condition from fully developed, with only the embryo sac defective, to a mere dried remnant (fig. 21).

Conclusions as to significance of degenerations

Such degenerations as have been described look toward the complete elimination of either the stamens collectively or the carpels. The process seems very severe, and results in a high mortality, not only of flowers, but of the developing fruits as well. It is a case of degeneration during the process of development, and is not to be confused with arrested development, such as occurs in the production of staminodia, and which looks toward reduction in the number of organs in the cycle involved.

The term dioecism has a very different meaning when applied to spermatophytes and when applied to cryptogams. In the latter it is assumed that separation of the sexes to distinct male and female gametophytes is a phenomenon based on heredity, and determined by chromatic constitution, and that the separation

occurs during the reduction divisions. When the differentiation is pushed farther back, however, until the sporophytes producing the two kinds of spores are likewise differentiated, it is difficult to see how chromatic constitution can be made to explain the situation. It is to this later and secondary phase of sex segregation that the term dioecism is applied in seed plants. The view has been expressed in scattered papers that the particular species under investigation have been rendered diclinous by failure of either the stamen or the ovules to produce functional gametophytes, and that this process has been carried a step farther, to the complete suppression of the functioning stamens in some (ovulate) plants, and to the complete suppression of functioning ovaries in other (staminate) plants. This view has been occasioned by the discovery that more or less perfect essential organs may produce few or no functional sexual products.

Rumex seems a particularly favorable group for the study of this process, and it is believed that it shows convincing evidence for the origin of dicliny, and finally of dioecism, by degenerations during ontogenesis. The members of the section LAPATHUM, including *R. crispus*, are variously described in manuals as having hermaphrodite, polygamo-monoecious, polygamo-dioecious, andromonoecious, gyno-dioecious, etc., flowers, while those belonging to the ACETOSA section are described as dioecious. In *R. crispus*, at least, the appearance of the mature flowers evidently is misleading, for sections show that the apparently perfect flowers are almost invariably functionally staminate; the apparently staminate flowers are really such; while the apparently ovulate may be either functionally ovulate or completely sterile. These conditions are brought about by degeneration at various stages in oogenesis and spermatogenesis, and not by arrested development. The result, even in the seemingly perfect flowers of *R. crispus*, is physiological dicliny.

ROTH (**8**) found in species of section ACETOSA, which are usually exclusively dioecious, that sometimes hermaphrodite and even staminate flowers are produced, but that the pollen is defective in every case; others have found the same situation. All the species in section LAPATHUM that he investigated produced hermaphrodite

flowers at first, and ovulate flowers almost exclusively later in the season. He found numerous instances of degenerating embryo sacs in *R. Acetosa*. I have examined a great many sections of *R. Acetosella*, and found no instance of such behavior. It would seem that degenerations in the ovary are much less frequent in the dioecious species than in the so-called hermaphrodite, and that when the ovulate plants occasionally produce stamens, all the pollen is functionless.

The conclusion is that *Rumex* formerly produced only hermaphrodite flowers, and that by degenerations in the stamens and in the carpels the condition has been attained such as is found in *R. crispus*, and the species of section LAPATHUM in general, where the inflorescence contains a mixture of physiologically staminate, physiologically ovulate, a few bisporangiate, and many completely sterile flowers. This is physiological dicliny. The process has been carried farther in some forms, resulting in segregation of the staminate and ovulate flowers to separate plants, as is now the case in the species in section ACETOSA. That these latter forms have been derived from bisporangiate or monoecious ancestors is indicated by the occasional production of stamens on "ovulate" plants. That this derivation has been due to degenerations is indicated by the sterility of the staminate structures when they are formed.

It seems clear that the stamens are more readily eliminated from the flowers than are the ovules. They start degenerating earlier in their development, and it is very common for all trace of them to be lost by the time the flower opens, while the ovules invariably persist in physiologically staminate flowers, and very frequently are defective only in the embryo sac.

It is probable that the degeneration processes favor the occurrence of apogamy. Not only does degeneration result in elimination of stamens from many flowers, but it results also in sterility of the pollen that is produced by normal anthers. Dioecism would render pollination by the small amount of pollen remaining normal a very uncertain process. Finally, it is altogether possible that when the degeneration process in the ovary is but weakly manifested, it may interfere with reduction in the megaspore mother

cell, and may account for the long wait in the prophase of the heterotypic mitosis, and the subsequent completion of the division as a typic mitosis, as has been repeatedly reported for well marked apogamous plants.

The strong tendency to failure in the sexual process may also contribute to the development of highly successful methods of vegetative propagation. Nearly all the species of section LAPATHUM perennate by strong storage tap roots crowned by a short stem region, or by storage rhizomes, and all propagate very freely by detached fragments of these underground stems. *R. Acetosella* propagates by long lateral roots which produce new plants at intervals. It is a striking fact that patches of the plant are dense growths of almost exclusively staminate or ovulate plants. This is what would be expected to result from such vegetative propagation, and would be a curious segregation to result from plants produced to any great extent from seeds. All the evidence I have seen points to apogamy in *R. Acetosella;* seed production is very scanty in proportion to the number of flower buds, and a large percentage of the fruits are empty. A considerable number of seedlings scattered about in patches of ovulate plants indicates that many of the seeds are viable.

From the great number of diclinous angiosperm flowers that contain remnants of the other organs, it seems very probable that the degeneration processes here described are of widespread occurrence, and are scattered throughout the group from the lowest to the highest forms. It is planned to make a study of dicliny in the future, in the effort to substantiate or disprove this theory of the origin of dicliny as the result of degenerations.

The cause of these degenerations is not known. The few authors who have discussed the problem all agree that faulty nutrition is important, if not as the direct cause, at least in producing conditions that call the phenomenon into activity. HOFFMANN (5) supposed that the embryos of *R. Acetosella* and other dioecious plants are sexless, and that sex is determined in the early stages of the seedling by the conditions under which they germinate. GÄRTNER (4) used the evidence in the reverse order, and thought

that degenerations in the stamens and ovules are "caused by the inherent tendency in the species to become dioecious." "Faulty nutrition" is so indefinite and vague, and includes such a wide range of possibilities that it can scarcely be considered as an adequate explanation. It is more probably a condition which calls into greater activity certain fundamental and at present unknown causes of degeneration that are always present in a wide range of angiosperm forms. It is barely possible that the peculiar detached vascular bundle of the ovule may be responsible for the failure of the ovule in later stages. This bundle never has been found connected with the general vascular system of the peduncle, even in those infrequent instances when the embryo and endosperm seem to be developing normally. If this should prove to be the immediate cause for later degenerations in the ovule, there still remains no hint of the cause for the failure of the ovular vascular bundle to make proper connections.

STRASBURGER (10) concluded from his study of the species of EUALCHEMILLA that sterility is the result of excessive mutation. It seems clear that sterility, partial or complete, results from degenerations, and probably such degenerations are the *only* morphological causes of sterility. It might follow then that excessive mutation is the cause of sterility, or it may be that mutating species are only more susceptible to degenerations.

JEFFREY (6) believes that sterility is the result of hybridization. Again, it is a question whether hybridity is a fundamental cause, or only produces physiological conditions that activate a more or less latent tendency to degenerations. If hybridity is the underlying cause of the degenerations that lead to sterility, and the theory that these degenerations lead to dicliny, apogamy, and the development of successful methods of vegetative propagation should prove to be correct, it would seem to follow that all hybrids are tending toward these states. Probably the evidence would not support this reasoning. It is more probable that there exists no causal relation between the hybrid state and degenerations, except as physiological conditions in hybrids favor such processes.

DORSEY (2) concludes from a study of grape hybrids that "hybridity is not necessarily a cause of sterility," and that "pollen

sterility in the grape is only a step toward functional dicliny." All the scanty published evidence I have seen seems to support this conclusion.

Summary

1. Organogeny is normal, with slight delay in appearance of petals and carpels.

2. The megaspore mother cell produces a tetrad of megaspores, the innermost of which functions. The haploid chromosome number is 32.

3. The embryo sac is of the ordinary 8-nucleate type.

4. Microsporogenous tissue is formed from the primary sporogenous cell by 3–4 successive divisions, and reduction is normal. The haploid chromosome number is 32.

5. The mature pollen grain contains two male nuclei, the progeny of a definite generative cell.

6. There is good negative evidence both for and against the occurrence of fertilization. This raises the question whether some of the megaspore mother cells may not undergo reduction, while others only simulate reduction and give rise to a diploid embryo sac, the latter *only* producing embryos by the apogamous development of the egg.

7. Widespread degenerations occur: (*a*) in any or all of the anthers, at any stage from the sporogenous initial to the mature pollen grain, and may involve only the sporogenous tissue and its products, or the entire anther; (*b*) in the ovary, at any stage from the functioning megaspore to the maturing fruit, and may involve only the embryo sac, or both embryo sac and ovule, or the entire ovary; (*c*) in entire inflorescences.

8. Most pollen grains undergo cytolysis, with abundant starch formation, conspicuous enlargement, and the formation of "pollen tubes."

9. Only a small percentage of pollen grains and embryo sacs have the appearance of being functional.

10. An unidentified fungus invades the anthers after dehiscence, ramifying among but rarely penetrating the pollen grains.

11. There is a definite abscission layer near the base of the peduncle, cutting off either before or after blooming those flowers

in which both stamens and ovary are early involved in strong degenerations. There is also a degeneration of the filament cells, severing the maturing anthers.

12. Four types of mature flowers are produced by these degenerations: (*a*) physiologically staminate, although the pollen may or may not be functional (the ovary is functionless); (*b*) physiologically ovulate, the stamens having been completely eliminated by degeneration; (*c*) bisporangiate, having both stamens and ovary functional (very rare); (*d*) completely sterile, having functionless ovary, and stamens completely eliminated.

13. It is suggested that these degenerations may be of widespread occurrence, and probably are the cause of (*a*) dicliny, and finally dioecism, and (*b*) apogamy, and that (*c*) they favor the development of successful methods of vegetative propagation.

14. The cause of such degenerations is as yet unknown. It is suggested that deficient nutrition, excessive mutation, and hybridity bear no causal relation to degeneration, except as they may create physiological conditions favorable for it.

I wish to thank Dr. J. M. COULTER, Dr. C. J. CHAMBERLAIN, and Dr. W. J. G. LAND for their interest and assistance throughout the course of this investigation.

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EXPLANATION OF PLATES XVII–XIX

Figs. 22–75 were all drawn at an initial magnification of ×1460, with the exception of figs. 26 and 60, which were ×4400; all figures have been reduced one-half.

FIG. 22.—Longitudinal section of young nucellus, showing archesporial cell terminating a definite axial row.

FIG. 23.—Archesporial cell divided into primary wall cell and megaspore mother cell.

FIG. 24.—Nucellus with 2 megaspore mother cells, both in prophase of heterotypic mitosis.

FIG. 25.—Megaspore mother cell in prophase of heterotypic mitosis; wall cells have divided periclinally.

FIG. 26.—Diakinesis in megaspore mother cell, showing 32 pairs of chromosomes, the haploid number; reconstructed from 3 sections.

FIG. 27.—Spindle of heterotypic mitosis in megaspore mother cell; plasmolysis may possibly indicate initial stage of degeneration.

FIG. 28.—Normal tetrad of megaspores.

FIG. 29.—Early degeneration of outer 3 megaspores of tetrad.

FIG. 30.—Inner cell has preceded outer in homoiotypic mitosis.

FIG. 31.—Early degeneration of functioning megaspore.

FIG. 32.—Degeneration of functioning megaspore at a slightly later stage.

FIG. 33.—Normal growth of functioning megaspore.

FIGS. 34, 35.—Normal functioning megaspores fully enlarged.

FIGS. 36, 37.—Degeneration of fully enlarged functioning megaspores.

FIG. 38.—Normal 2-nucleate stage of embryo sac.

FIG. 39.—Early stage in degeneration of embryo sac in 2-nucleate stage.

FIGS. 40, 41.—Same, more advanced.

FIG. 42.—Normal 4-nucleate stage of embryo sac.

FIG. 43.—Degeneration of embryo sac in 4-nucleate stage.

FIG. 44.—Normal 8-nucleate stage of embryo sac just beginning mature organization.

FIG. 45.—Degeneration of embryo sac in 8-nucleate stage.

FIG. 46.—Normal fully developed embryo sac.

FIG. 47.—Fully developed embryo sac in advanced degeneration, apparently after a long wait for fertilization.

FIG. 48.—Transverse section of portion of a young anther, showing archesporial cells.

FIG. 49.—Archesporial cell divided into primary parietal cell and primary microsporogenous cell.

FIG. 50.—Primary microsporogenous cells beginning to degenerate; anticlinal division preceded usual periclinal in archespore.

FIG. 51.—Primary microsporogenous cell in advanced degeneration.

FIG. 52.—First division in normal primary microsporogenous cell.

FIG. 53.—Degeneration restricted to a single cell (in transverse section) of early microsporogenous tissue.

FIG. 54.—Degeneration of isolated cells in later microsporogenous tissue.

FIG. 55.—Advanced degeneration of entire mass of microsporogenous cells; wall cells are also involved.

FIG. 56.—Same at a later stage of development; wall cells nearly normal.

FIG. 57.—Portion of normal anther at synapsis of microspore mother cells.

FIG. 58.—Same stage, with premature degeneration of tapetum.

FIG. 59.—Same stage, with microsporogenous tissue completely disorganized; middle wall layer and tapetum greatly enlarged.

FIG. 60.—Diakinesis stage of heterotypic mitosis in normal microspore mother cell, showing 32 pairs of chromosomes, the haploid number; reconstructed from 2 sections.

FIG. 61.—Transverse section of loculus of collapsed anther, in which degenerating sporogenous tissue has just completed reduction; tapetum shows variety of nuclear situations, and is still functional.

FIG. 62.—Tetrad of microspores in various stages of degeneration.

FIG. 63.—Probably normal disorganization of tapetum at a time when the microspores are well differentiated, although apparently beginning to degenerate.

FIG. 64.—Apparently normal microspore.

FIG. 65.—Microspore degenerating.

FIG. 66.—Microspore with walls completely differentiated, in advanced degeneration.

FIG. 67.—Apparently nearly normal pollen grain with generative cell organized.

FIG. 68.—Same, showing beginning of hypertrophy and starch accumulation.

FIG. 69.—Hypertrophied pollen grain, packed with large starch grains.

FIG. 70.—Hypertrophied pollen grain with contents beginning to disorganize, penetrated by a fungus hypha.

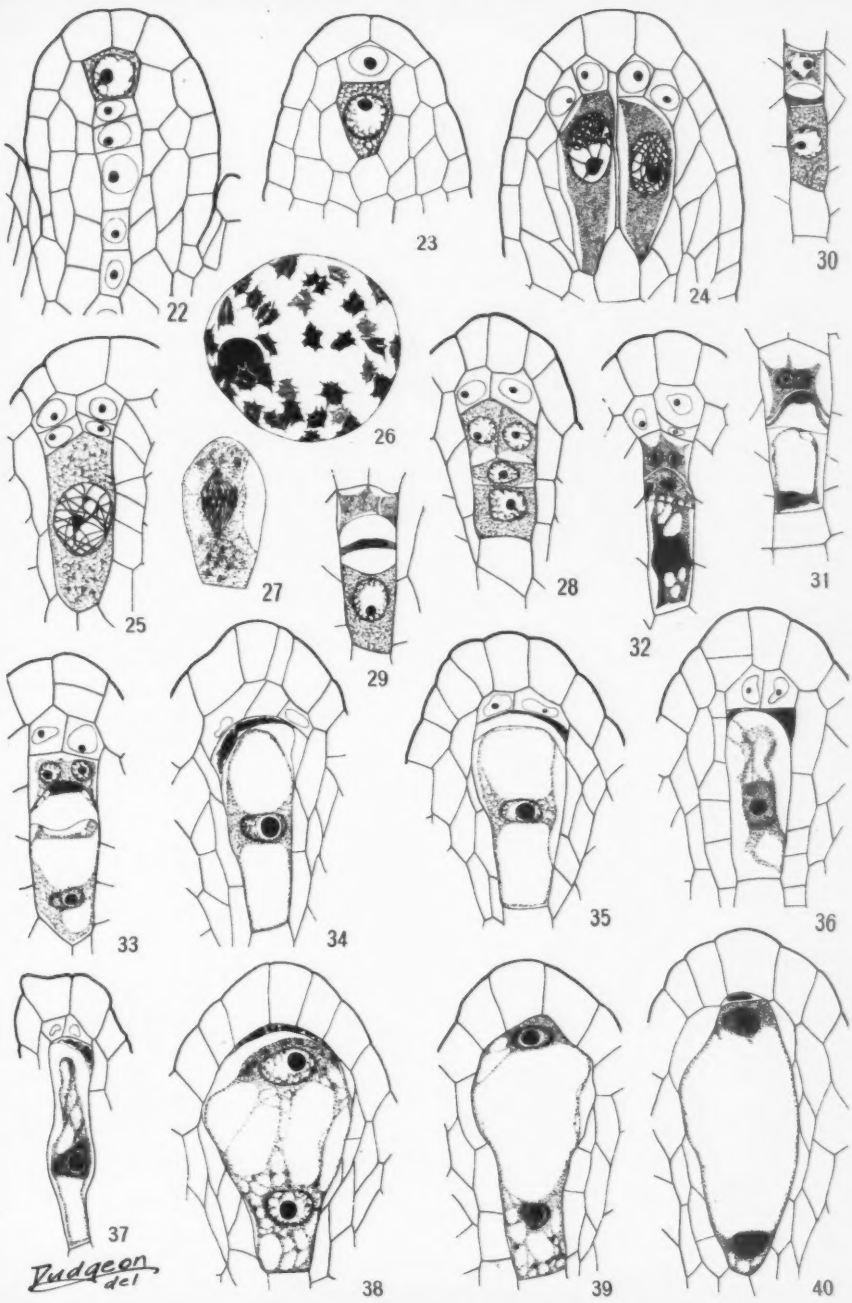
FIG. 71.—Hypertrophied pollen grain with contents in advanced disorganization.

FIG. 72.—Same, with beginning of pollen tube formation.

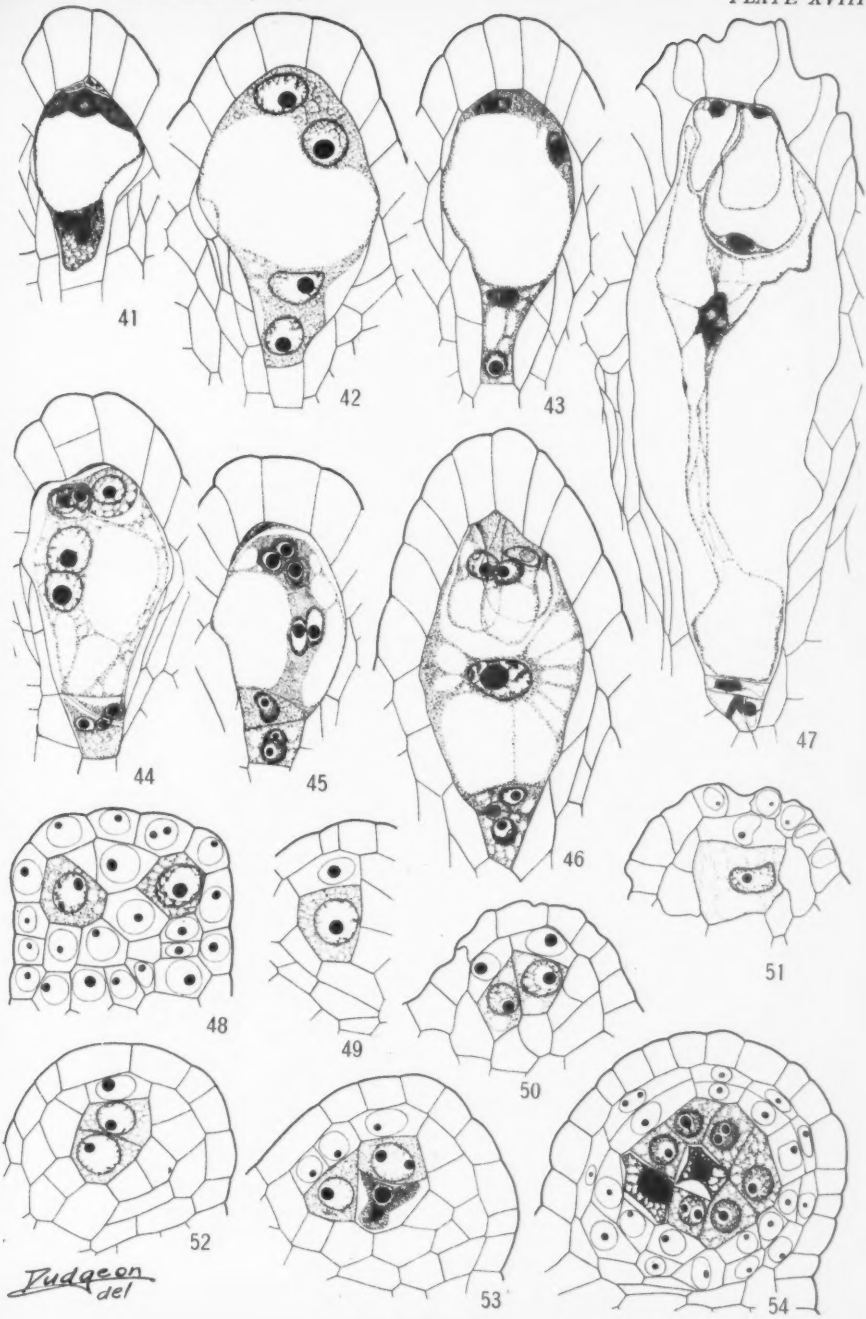
FIG. 73.—Hypertrophied pollen grain, with contents disorganized to homogeneous mass and beginning to collapse.

FIG. 74.—Portion of hypertrophied pollen grain with well developed pollen tube; disorganized nuclei still in grain.

FIG. 75.—Hypertrophied pollen grain with long pollen tube into which remains of disorganized nuclei have migrated.



DUDGEON on RUMEX



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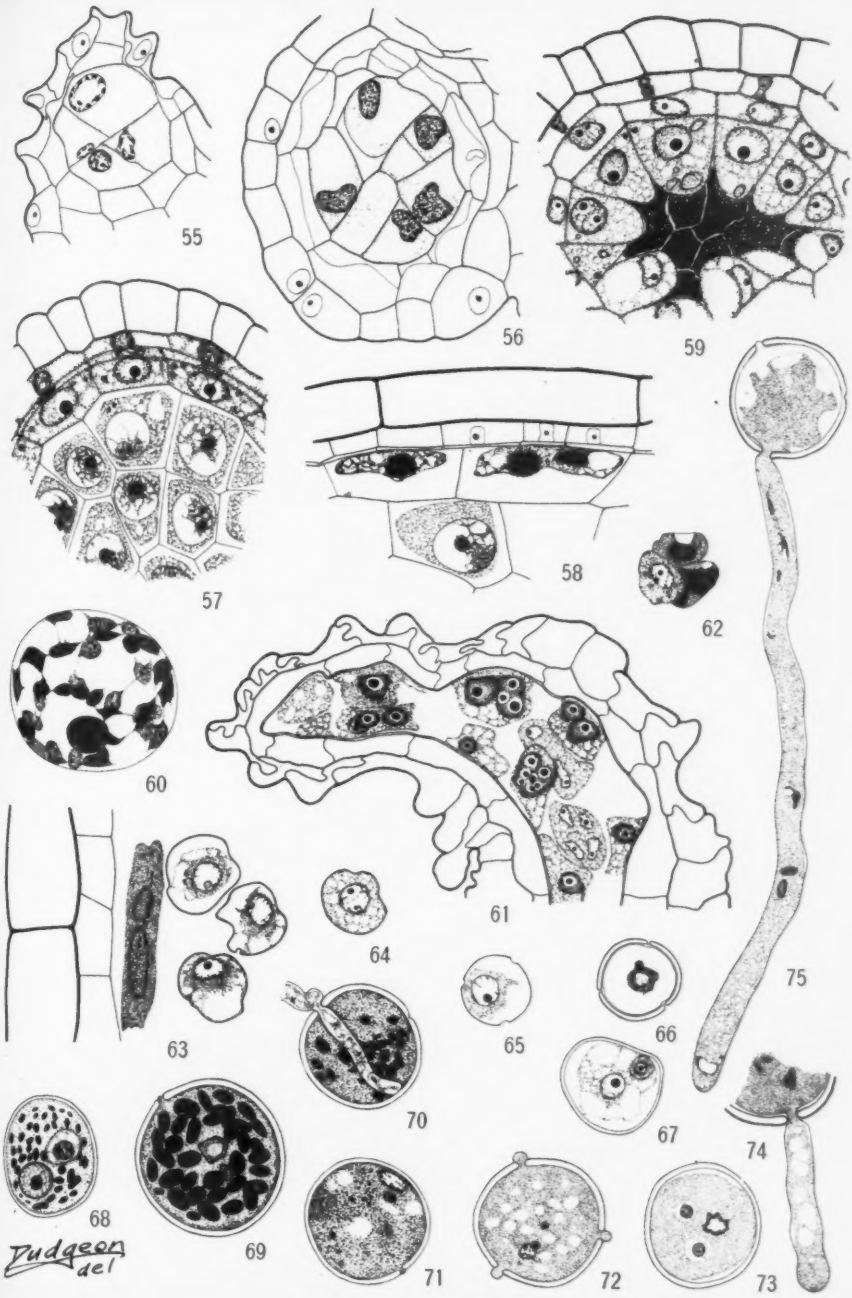

DUDGEON on RUMEX

NOTES ON NORTH AMERICAN TREES. III. TILIA. I

C. S. SARGENT

The results of a study of the lindens of the United States carried on for a number of years will be found in these notes. It is based on observations of these trees in the forest and the examination of a large collection of herbarium material gathered in all parts of the country where lindens grow.

To understand a species of *Tilia* properly 4 collections are needed: the first made in early spring to show the unfolding leaves, the second in early summer when the trees are in flower, the third 6 or 8 weeks later when the fruit is mature, and the fourth in winter for the winter buds. Many of these trees grow in regions where summer collecting presents many difficulties and causes much discomfort; the trees do not always flower every year, and the fruit often does not mature or is destroyed in storms before it is ripe. It is not surprising, therefore, that American lindens are poorly represented in the older herbaria and that botanists depending on collections in herbaria have not been able to obtain a comprehensive idea of the representatives of the genus in this country.

Even with abundant material it is difficult to find characters by which the different species and their varieties can be satisfactorily arranged. In most of the large genera of trees many of the species can be distinguished by the bark, but the bark of the American lindens varies so little that it has no value in determining species. The branchlets of some species are stouter than others, but stout and slender branchlets are often found on the same tree. Their color is uniform on some species, but on others varies from yellow or pale brown to red; on some species the branchlets are glabrous and on others they are pubescent, but in some species glabrous and pubescent branchlets are found on the same tree. In a few species a good character is found in the winter buds, but on other species the buds may be glabrous or pubescent. Except in size, there is no constant character in the flowers, and the fruit, although it varies

slightly in size, is always globose, depressed-globose, slightly ovoid, or ellipsoidal, fruits of these different forms occurring in the same species and some of them on the same tree. The shape and size of the leaves vary on different branches of the same tree, but their serration and venation have sometimes specific importance. The only constant and reliable character, however, which I have found for distinguishing the species is in the absence or presence of the hairy covering on the surface of the leaves and in the nature of this covering when it exists, and the following arrangement of the species is based on these characters. The color of the hairs, however, cannot be depended on; on some species the hairs on the lower surface of the leaves are constantly white, but in other species they are brown or white on different trees, and on others they are white on the leaves of lower branches and brown on those of upper branches. When it is possible to make a comparative study of the trees growing together in an aboretum where they can be watched through the year it will probably be found that some of the characters which now seem constant cannot be depended on and that another arrangement of this group will be necessary.

Unfortunately the lindens first known from North America were described in Europe, often from cultivated trees, and the material on which these descriptions were made was insufficient and is often no longer in existence. There is therefore still some uncertainty in regard to the correct names of a few species.

I take this opportunity to express my sincere thanks to Mr. T. G. HARBISON, Professor R. S. COCKS, and Mr. E. J. PALMER, who have patiently and industriously collected *Tilia* material for the Arboretum and made possible these notes.

CONSPECTUS OF THE SPECIES OF THE UNITED STATES

Surface of the leaves glabrous at maturity.

Leaves glabrous or almost glabrous when they unfold, coarsely serrate.

Leaves furnished with conspicuous tufts of axillary hairs, their lower surface light green and lustrous; pedicels glabrous or nearly glabrous
1. *T. glabra*

Leaves usually without tufts of axillary hairs, their lower surface not lustrous; pedicels densely hoary tomentose.....2. *T. nuda*

Leaves hoary tomentose when they unfold.

Leaves soon glabrous.

Leaves coarsely serrate with stout teeth, their veinlets conspicuous; branchlets stout, bright red ..... 3. *T. venulosa*

Leaves finely serrate with straight or incurved teeth, their veinlets less conspicuous; branchlets slender, pale reddish brown .. 4. *T. littoralis*

Leaves crenately serrate, glaucescent on the lower surface 5. *T. creno-serrata*

Leaves covered below early in the season with articulate hairs, becoming glabrous or nearly glabrous.

Leaves thin, coarsely serrate, green or glaucescent on the lower surface, with or without tufts of axillary hairs; summer shoots not pubescent 6. *T. floridana*

Leaves subcoriaceous, finely serrate, bluish green and lustrous below early in the season; tufts of axillary hairs minute, usually wanting; summer shoots pubescent ..... 7. *T. Cocksii*

Surface of the leaves pubescent below during the season.

Lower surface of the leaves covered with short gray firmly attached pubescence; tufts of axillary hairs not conspicuous ..... 8. *T. neglecta*

Lower surface of the leaves covered with articulate easily detached hairs.

Branchlets without straight hairs.

Leaves ovate, acuminate, usually obliquely truncate at base, glabrous above, their pubescence brownish or white ..... 9. *T. caroliniana*

Leaves oblong-ovate, cordate or obliquely cordate at base, pubescent above early in the season ..... 10. *T. texana*

Leaves semiorbicular to broadly ovate, abruptly short-pointed, deeply and usually symmetrically cordate at base ..... 11. *T. phanera*

Branchlets covered with straight hairs; leaves ovate, abruptly short-pointed, oblique and truncate at base ..... 12. *T. lasioclada*

Surface of the leaves tomentose below during the season with close firmly attached tomentum.

Tomentum white, gray, or brown; leaves usually glabrous on the upper surface; branchlets and winter buds glabrous (occasionally pubescent in varieties of no. 13).

Branchlets slender; petioles not more than 4 cm. long; leaves oblong-ovate, acuminate or abruptly pointed, oblique and truncate or cordate at base; tomentum on the leaves of upper branches often brown; flowers 3.5–5 mm. long ..... 13. *T. heterophylla*

Branchlets stout; petioles up to 7 cm. in length; leaves oblong-ovate, acuminate, obliquely truncate at base; tomentum always white; flowers 10–12 mm. long ..... 14. *T. monticola*

Tomentum pale or brownish; leaves thickly covered above early in the season with fascicled hairs; branchlets tomentose; winter buds pubescent 15. *T. georgiana*

1. TILIA GLABRA Vent.—*Tilia americana* var. a *densiflora* V. Engler, Monog. Tilia, 137 (in part). 1909; *Tilia americana* var. *densiflora* f. *megalodonta* V. Engler, l.c. 139. 1909; *Tilia americana* var. *densiflora* f. *laxiflora* V. Engler, l.c. 140. 1909.—For the northern lime tree with glabrous leaves the name *Tilia americana* has been adopted in recent years by all authors who have written on American trees. LINNAEUS, however, based his species on the *Tilia floribus nectariis instructis* of KALM, quoting as synonyms of KALM's species the *Tilia foliis majoribus mucronatis* of CLAYTON and the *Tilia amplissimis glabris foliis, nostrati similis* of PLUKENET Mant. 181. KALM's specimen is not in the Linnaean Herbarium, and it is impossible to identify it from the description, which applies as well to anyone of the 3 species which KALM may have seen. Indeed both *T. neglecta* and *T. heterophylla Michauxii* are more common in the part of the country which he visited than the tree which recent authors have called *T. americana*, and it is impossible to identify KALM's plant. CLAYTON's description cannot be applied to the northern glabrous tree, for it is not known to grow in CLAYTON's region; and as it is impossible to determine if more than one species was included in LINNAEUS' *T. americana* or, if the name was applied only to one species, what that species was, it seems necessary to give up entirely the name of *T. americana* Linnaeus. This name was taken up by MILLER in the eighth edition of *The Gardener's Dictionary*, but the leaves of MILLER's *T. americana* are described as "subtus pilosis," and his species is probably the *T. neglecta* of SPACH, which is now known to be an old inhabitant of European gardens. AITON's description in the *Hortus Kewensis*, "*T. floribus nectario instructis, foliis profundis cordatis argute serratis glabris*," well describes the northern glabrous tree, although he follows LINNAEUS in calling it a native of Virginia and Canada. The *T. caroliniana* of MARSHALL but not of MILLER is probably the northern tree, and his *T. americana* with leaves a little hairy underneath is evidently *T. neglecta*, which is the common species in MARSHALL's region. If the *T. americana* of LINNAEUS is rejected, it is necessary to determine what name should be adopted for it. The next name used for this tree is *T. glabra* of VENTENAT, published in 1800, and this seems to be the name which should be adopted

for it, as it was by NUTTALL, DECANDOLLE, HOOKER, DARLINGTON, and other authors. In his description VENTENAT speaks of the leaves as "d'abord légerement pubescent, ensuite parfaitement glabre," which is correct, for although the young leaves are often entirely glabrous they are sometimes furnished for a few days after they unfold with scattered articulate hairs on the upper surface and on the lower surface with soft pale hairs which are most abundant on the midribs and veins.[1]

2. **Tilia nuda,** n.sp.—*Tilia pubescens* var. a *Aitonii* V. Engler, Monog. Tilia, 128 (in part). 1909; *Tilia americana* var. a *densiflora* V. Engler, l.c. 137 (insomuch as relates to Houston, Texas). 1909; *Tilia americana* probably of many authors but not of LINNAEUS.—Leaves thin, ovate, abruptly pointed at apex, obliquely truncate or unsymmetrically cordate at base, coarsely serrate with long, slender, straight, or slightly curved, conspicuously glandular teeth; as they unfold, dark red and sparingly pubescent on the midribs and veins, glabrous at the end of a few days, without or very rarely with small axillary tufts, dark green on the upper surface, pale yellow-green on the lower surface, 10–12 cm. long, 7–9 cm. wide; petioles slender, glabrous, 5–6 cm. in length. Flowers 8–10 mm. long, on hoary tomentose pedicels, in broad usually 10- or 12- sometimes 30- or 40-flowered long-branched glabrous corymbs; peduncle glabrous, the free portion 2–3 cm. in length, the bract glabrous, oblong, often slightly falcate, cuneate or rounded at base, rounded at apex, short-stalked, 1–3 cm. wide; sepals acute, rusty tomentose on the outer surface, glabrous on the inner surface; petals oblong-ovate, narrowed at the rounded apex; staminodia oblong-obovate, rounded at the broad apex, style glabrous. Fruit subglobose to depressed-globose, covered with rusty tomentum, 6–7 mm. in diameter.

[1] VENTENAT'S paper on *Tilia* was read in 1799 and published in 1802 in the fourth volume of the *Mémoires de l'Acad. Sci. Paris.* A separate of this paper with the same pagination appeared the same year, but a Spanish translation without the illustrations was published in Madrid in May 1800 with the title *Monografia del género Tilo* in the second volume of the *Anales de Historia Natural.* The correct citation, therefore, of VENTENAT'S American species is *T. glabra* Ventenat in An. Hist. Nat. **2**:62. 1800; *T. pubescens* Ventenat in An. Hist. Nat. **2**:63. 1800; *T. pubescens* var. *leptophylla* Ventenat in An. Hist. Nat. **2**:64. 1800; *T. heterophylla* Ventenat in An. Hist. Nat. **2**:65. 1805.

Usually a small tree with pale furrowed or sometimes checkered bark, small spreading branches forming a narrow round-topped head, and slender glabrous orange or red-brown branchlets. Winter buds ovate, obtusely pointed, dull red, glabrous, 4–5 mm. long. Flowers usually in the first week of June before the other species with which it is associated. Fruit ripens in September.

MISSISSIPPI.—Rich woods and river bluffs near Natchez, Adams County, *Miss C. C. Compton*, June 2 and September 24, 1915 (no. 12 type), May and September 1915 (no. 13); Clifton Upper Bluff, *Miss Compton*, May 18, June 2, and September 24, 1915 (no. 2); Kingston Road, near Natchez, *Miss Compton*, August 26, 1915; Fenwick, Adams County, Miss *Compton*, April 17, 1915; bluff of the Mississippi River above Natchez, *C. S. Sargent*, April 8, 1913, April 17, 1915, and April 17, 1916; Woodville, Wilkinson County, *C. S. Sargent*, April 15, 1916; near Jackson, Hinds County, *T. G. Harbison*, May 17, 1915 (no. 63), September 19, 1915 (no. 63A), May 22, 1915, September 18, 1915 (nos. 84, 88A); Bolton, Hinds County, *T. G. Harbison*, May 24, 1915.

ALABAMA.—Hatcher's Creek, Berlin, Dallas County, *R. S. Cocks*, June 6, July 28, 1916 (no. 950).

LOUISIANA.—St. Francisville, West Feliciana Parish, *C. S. Sargent*, April 12, 1916; Lake Charles, Calcasieu Parish, *R. S. Cocks*, May 21, July 7, 1915 (no. 2530), May 21, 1915, *C. S. Sargent*, April 12 and 13, 1915, *E. J. Palmer*, May 16, September 11, 1915 (nos. 7644, 8523).

TEXAS.—White Oak Bayou, Houston, Harris County, *F. Lindheimer*, March 1840 (no. 10779 in Herb. Missouri Bot. Gard.), *E. J. Palmer*, May 17, September 15, 1917 (nos. 11397, 12763); Livingston, Polk County, *E. J. Palmer*, October 7, 1914 (nos. 6753, 6755), September 12, 1916 (no. 10696), April 4, September 17 and 19, 1917 (nos. 11467, 12016, 12796, 12797, 12798, 12803); Marshall, Harrison County, *E. J. Palmer*, October 17, 1914 (no. 6852), April 18, 1915 (no. 7277), June 8, 1915 (no. 7912); Larissa, Cherokee County, *B. F. Bush*, October 7, 1909 (no. 5977), *E. J. Palmer*, June 3, September 22, 1915 (nos. 7846, 8622); Liberty, Liberty County, *E. J. Palmer*, May 22, 1915 (no. 7736); San Augustine, San Augustine County, *E. J. Palmer*, September 7, 1916 (no. 10627); College Station, Brazos County, *E. J. Palmer*, April 28, 1917 (no. 11722); Huntsville, Walker County, *E. J. Palmer*, May 26, 1917 (no. 12046).

ARKANSAS.—Fulton, Hempstead County, *B. F. Bush*, April 5, 1909 (no. 5464A); McNab, Hempstead County, *E. J. Palmer*, June 18, 1915 (no. 8056), September 8, 1917 (no. 12674).

On this tree as it grows in the neighborhood of Natchez, where it is common, the bracts of the peduncles vary from 1 cm. up to 3 cm. in width. In *Miss Compton's* no. 12 the bracts are sometimes almost sessile or are borne on stalks of varying length up to 3 cm. At Larissa, Texas, trees growing on sandy moist hillsides are often 25–30 m. high, with trunks 75 cm. in diameter covered with deeply fissured bark. The absence of pubescence from the young leaves and the absence of axillary hairs well distinguish this species, but the absence of

the axillary tufts cannot always be depended on, for occasional trees have been found in Louisiana and Alabama on which some of the leaves are furnished with these tufts (Louisiana, near Alexandria, Rapides Parish, *R. S. Cocks*, June 1905; Wakefield, West Feliciana Parish, *R. S. Cocks*, June 1905. Alabama, near Selma, Dallas County, *R. S. Cocks*, June and July 1914, June 2, July 12, 1915 [no. 784], April 20, July 25, 1916 [nos. 822, 960]).

A form of this tree with leaves more or less pale on the lower surface may be distinguished as

TILIA NUDA var. **glaucescens,** n.var.—Differing from the type in the glaucous lower surface of the leaves.

ALABAMA.—Bluffs of the Alabama River, Berlin, Dallas County, *R. S. Cocks*, June 11, July 20, 1915 (no. 786 type).

LOUISIANA.—Lake Charles, Calcasieu Parish, *R. S. Cocks*, May 21, 1915 (no. 2534); Natchitoches, Natchitoches Parish, *E. J. Palmer*, May 10, June 9, 1915 (nos. 7569, 7923), June 9, 1915 (no. 7923).

OKLAHOMA.—Page, Le Flore County, *E. J. Palmer*, July 27, 1917 (no. 12638).

TEXAS.—Marshall, Harrison County, *E. J. Palmer*, June 8, 1915 (nos. 7909, 7912); San Augustine, San Augustine County, *E. J. Palmer*, June 5, 1915 (no. 7880).

Like the green-leaved type, the trees of this variety differ in the size of the leaves, in the pedunculate bract which on *Palmer's* no. 7923 from Natchitoches is 8 cm. wide, while on his no. 7909 from Marshall it is only 3.5 cm. wide. The number of flowers in a corymb is equally variable. The tomentum on the fruit of *Cock's* no. 786 from Sardis, which is the only fruit of the variety which I have seen, is paler than that on the fruit of the green-leaved form.

TILIA NUDA var. **brevipedunculata,** n.var.—Differing from the type in the serration of its smaller leaves glaucescent below, in the shorter free portion of the peduncles of the inflorescence, and in its broader bract. Leaves ovate, gradually or abruptly narrowed and acuminate at apex, obliquely and unsymmetrically cordate or rounded at base, finely crenately serrate with gland-tipped teeth, smooth and dark yellow-green on the upper surface, pale yellow-green and glaucescent on the lower surface, glabrous, 7–8 cm. long and 5 or 6 cm. wide; petioles slender, glabrous, 2–2.5 cm. in length. Flowers 5 or 6 mm. long, on pubescent pedicels, in compact, mostly 10–20-flowered, sparingly pubescent corymbs; peduncle sparingly pubescent, the free portion only about 1.5 cm. in length, the bract broad and rounded or unsymmetrically cuneate at base, rounded

or acute at apex, nearly sessile or short-stalked, glabrous with the exception of occasional fascicled hairs on the upper side of the midrib, 7–8 cm. long and 3–3.5 cm. wide, much longer than the peduncle; sepals acute, covered on the outer surface with pale pubescence and on the inner surface with soft white hairs; petals oblong-ovate, acuminate, a third longer than the sepals; staminodia obovate, gradually narrowed and cuneate at base, acute at apex. Fruit not seen.

A tree 8–10 m. high, with slender, glabrous, dark red-brown branchlets. Flowers the first week of June.

Flat wet woods subject to overflow, San Augustine, San Augustine County, Texas, *E. J. Palmer*, June 5, 1915 (no. 7889 type).

This tree should perhaps be considered the type of a new species. So little is known of it, however, that in spite of the different serration of the smaller leaves and the remarkably short free portion of the peduncle of the inflorescence and its broader bract, it is perhaps now best considered a variety of *T. nuda*, which is common in eastern Texas.

3. **Tilia venulosa,** n.sp.—Leaves broadly ovate, abruptly acuminate at apex, cordate or unsymmetrically cordate or obliquely truncate or cordate at base, coarsely serrate, with gland-tipped teeth pointing forward; when they unfold, covered with pale tomentum, soon becoming pubescent and glabrous before the flowers open, dark yellow-green on the upper surface, paler on the lower surface, 10–14 cm. long and broad, with prominent pale yellow midribs slightly villose on the upper side near the base, and 9 or 10 pairs of remote primary veins without axillary tufts and connected by conspicuous cross veinlets; petioles stout, glabrous, 4.5–5 cm. in length. Flowers 8–9 mm. long, on slightly pubescent pedicels, in broad, slender-branched, nearly glabrous corymbs; peduncle stout, glabrous, red, the free portion 2.5–4 cm. in length, the bract nearly sessile, oblong to slightly obovate, gradually narrowed and rounded at base, rounded at apex, glabrous on upper surface, pubescent below along the midrib and veins, 3–4 cm. wide, longer than the peduncle; sepals ovate, acute, pale pubescent on the outer surface, villose on the inner surface and furnished at the base with a tuft of long white hairs, a third shorter than the lanceolate acuminate petals; staminodia oblong-obovate, rounded at apex, about as long as the sepals; stigma slightly villose at base. Fruit sub-

globose, 6–7 mm. in diameter, covered with loose light brown pubescence.

A tree 20–25 m. high, with stout, red, glabrous branchlets. Winter buds ovate, cylindrical, obtusely pointed, dark red, 7–8 mm. in length. Flowers during the first week of July. Fruit ripens the end of September.

Rocky "coves" in rich soil, Hickory Nut Gap, in the Blue Ridge, North Carolina, *W. W. Ashe*, April, May, and October 1916 (distributed as *T. eburnea* Ashe), *T. G. Harbison*, July 5 and September 21, 1917 (no. 2 type for flowers, no. 3 type for fruit); near Saluda, Polk County, North Carolina, *T. G. Harbison*, July 4, 1917 (nos. 1, 2, 4, 5, 7).

TILIA VENULOSA var. **multinervis,** n. var.—Differing from the type in its obliquely truncate, not cordate, leaves with 12 or 13 pairs of more crowded primary veins, ellipsoidal fruit, slender branchlets, and smaller winter buds.

A single tree near Saluda, Polk County, North Carolina, *T. G. Harbison*, July 4 and September 20, 1907 (no. 6 type).

T. venulosa is one of the handsomest of the American lindens as it is one of the most distinct. Its relationship is with *Tilia glabra*, from which it differs in the venation of the more constantly cordate leaves without axillary tufts, tomentose when they unfold, in the bright red peduncles, in the red branchlets, and in the larger red winter buds.

4. **Tilia littoralis,** n.sp.—Leaves ovate, unsymmetrical and rounded on one side and cuneate on the other, or symmetrical and cuneate or oblique and truncate at base, abruptly short-pointed and acute or acuminate at apex, finely serrate with straight or incurved glandular teeth; when they unfold, covered above with scattered fascicled hairs and tomentose below, soon glabrous, and when the flowers open, thin, yellow-green, paler on the lower than on the upper surface, 8–10 cm. long and 4.5–6 cm. wide, with slender midribs and primary veins and small conspicuous tufts of rusty brown axillary hairs; petioles slender, glabrous, 2.5–3 cm. in length; leaves on young vigorous shoots broadly ovate, truncate or slightly cordate at base, more coarsely serrate, pubescent with fascicled hairs especially on the midribs and veins, 10–12 cm. long and 8–9 cm. wide, their petioles densely pubescent. Flowers 7–8 mm. long, on pale tomentose pedicels, in small, compact, mostly 9–15-flowered, pubescent corymbs; peduncle covered with scattered

fascicled hairs, the free portion 1.5–2.5 cm. long, the bract sessile, gradually narrowed and cuneate at base, rounded at apex, ciliate on the margins, pubescent on the midribs, otherwise glabrous, 8–10 mm. wide, longer or shorter than the peduncle; sepals acuminate, pale pubescent on the outer surface, villose on the inner surface along the margins and at the base with long white hairs; petals acuminate; staminodia oblong-obovate, rounded at apex. Fruit ellipsoidal to depressed-globose, apiculate, covered with pale brown tomentum, 6–7 mm. in diameter.

A tree with slender glabrous branchlets densely coated when they first appear with pale pubescence, soon glabrous, light reddish brown during their first summer, often bright red during their first winter, becoming purple the following year and ultimately light gray-brown. Winter buds ovate, glabrous or puberulous, bright red, about 5 mm. long and 2–3 mm. in diameter.

Shore of Colonel's, formerly Bermuda, Island on Dyke's Creek, an ocean inlet near the mouths of the North Newport and Medway rivers near Dunham, Liberty County, Georgia, *Miss Julia King*, August 1, 1915, *T. G. Harbison*, September 8 and 9, 1916 (nos. 3, 6, 7), June 18, 1917 (no. 15 type).

This species, which I only know from one locality, is distinct in its small leaves, which are often symmetrical and cuneate at base, and are entirely glabrous with the exception of small conspicuous tufts of axillary hairs, in the small pedunculate bract, slender branchlets, and minute winter buds.

TILIA LITTORALIS var. **discolor,** n.var.—Differing from the type in the smaller leaves (7–8 cm. long) glaucous on the lower surface.

A single tree 17 m. high with a trunk 20 cm. in diameter, leaning over a salt water creek, Colonel's Island, with trees of the typical form and "very conspicuous among the other lindens near by on account of its glaucous leaves," *T. G. Harbison*, June 16, 1917 (no. 16 type).

5. **Tilia creno-serrata,** n.sp.—*Tilia floridana* Sargent, Man. 672 (in part at least) (not Small) *fig. 548.* 1903.—Leaves ovate, abruptly narrowed and acuminate at apex, usually oblique and unsymmetrically cordate or truncate or occasionally symmetrical and cordate at base, crenately serrate, the teeth tipped with minute glands; when they unfold, covered with pale caducous tomentum; at maturity dark green and lustrous above, glabrescent below, glabrous with the exception of minute axillary tufts of rusty hairs, mostly 9–12 cm. long and 7–8 cm. wide; petioles slender, glabrous about 3 cm. in length. Flowers 7–8 mm. long, on hoary tomentose

pedicels, in compact, mostly 10–18-flowered, tomentose corymbs; peduncle glabrous, the free portion 2.5–4 cm. in length, the bract oblong-obovate, cuneate at base, rounded at apex, short-stalked, glabrous, usually about 2 cm. wide; sepals acute, hoary tomentose on the outer surface, coated with pale tomentum, mixed with long white hairs on the inner surface; petals narrow-acuminate; staminodia oblong-obovate, notched at apex. Fruit ellipsoidal, conspicuously apiculate at apex, rusty tomentose, 8–10 mm. long and 6–8 mm. in diameter.

A tree 8–10 m. high, with a trunk 25–30 cm. in diameter, and slender, glabrous, red-brown branchlets. Winter buds ovoid, acute, dark dull red, glabrous, 4–5 mm. long. Flowers the middle of June. Fruit ripens from the middle to the end of August.

FLORIDA.—Sandy woods, Oviedo, Seminole County (type locality), *T. L. Mead*, May 15, 1887, June 15 and August 29, 1910; Lake Charm, Orange County, *T. L. Mead*, May 15, 1887, June 1910, *T. G. Harbison*, May 28, 1917 (nos. 3, 4, 5, 6); San Mateo, Putnam County, *T. G. Harbison*, June 15 and September 8, 1915 (nos. 3, 3a, 13, 14); Gainesville, Alachua County, *T. G. Harbison*, June 10, September 10, 1915 (nos. 5, 5A); Lake City, Columbia County, *T. G. Harbison*, April 22 and June 17, 1917 (no. 8); Micanopy Junction, Alachua County, *R. M. Harper*, April 14, 1910 (no. 146); Sumner, Levy County, *T. G. Harbison*, June 12, 1915, June 15, 1916, April 25, June 15, September 25, 1917.

GEORGIA.—Albany, Dougherty County, *T. G. Harbison*, June 25, 1915.

Harbison's Gainesville specimens have more coarsely serrate oblong leaves up to 10 cm. in length and are oblique at base. The bract of the peduncle is 3 cm. broad and in the broader corymbs there are 40–50 flowers. The leaves, however, are crenately serrate and quite glabrous with the exception of the small axillary tufts. This is evidently only a vigorous branch. On one of *Harbison's* San Mateo specimens the leaves in shape and serration resemble those of his Gainesville plant and the pedunculate bracts vary from 1 to 2.5 cm. in width. In the other San Mateo specimen the pedunculate bract is only 1 cm. wide. On *Harbison's* Albany specimen the pedunculate bract is only 5 mm. wide. The trees at San Mateo, Sumner, and Gainesville grow in low hummocks in sandy soil and sometimes attain the height of 20 m., with trunks 45 cm. in diameter.

6. TILIA FLORIDANA Ashe, Fl. Southern U.S. 761. 1903.—*Tilia pubescens* var. a *Aitonii* f. *glabrata*, Engler, Monog. Tilia, 129 (in part). 1909; *Tilia caroliniana* var. β *floridana*, Engler, l.c. 132. 1909.—The typical form of this species from Jackson County,

Florida, has broadly ovate, coarsely serrate, thin, acuminate leaves cordate or on leading shoots oblique at base, light green above and pale or green and covered early in the season on the under surface with fascicled hairs which soon disappear, so that when the flowers open they are glabrous or almost glabrous; they are often without tufts of hairs in the axils of the veins, or when these occur they are small, but on trees growing west of the Mississippi River they are more conspicuous. The flowers are 5–6 cm. long and are borne on hoary tomentose pedicels in few-flowered, rather compact, pubescent corymbs; in length the pedunculate bract varies from 6 to 13 cm. and in width from 1.2 to 3.5 cm., and the fruit is subglobose and covered with rusty tomentum. It is a tree with slender, glabrous, red-brown or yellow branchlets and small, obtuse, glabrous winter buds.

From western Florida this linden ranges to northern Georgia and to North Carolina, through the Gulf states to Texas, and through Arkansas to eastern Oklahoma and northern Missouri.

NORTH CAROLINA.—Polk County, *W. W. Ashe*, June 1875 (no. 102).

GEORGIA.—Cornelia, Habersham County, *T. G. Harbison*, September 30, 1916 (no. 5); Albany, Dougherty County, *T. G. Harbison*, June 25, 1915 (no. 2); cliffs of the Savannah River above Augusta, Richmond County, *C. S. Sargent*, March 30, 1908, *T. G. Harbison*, April 16, 1916 (no. 7); Shell Bluff, 30 miles below Augusta, *C. S. Sargent*, April 6, 1914.

FLORIDA.—Jackson County, *T. G. Harbison*, September 18 and 19, 1916 (nos. 3, 5, 6, 9, 11); near Mariana, *T. G. Harbison*, April 20, May 26 and 29, and June 29, 1917 (nos. 1, 7, 8, 20, 25, 32); River Junction, Gadsden County, *T. G. Harbison*, September 14, 1915; Sumner, Levy County, *R. M. Harper*, April 26, 1909 (no. 35).

ALABAMA.—Birmingham, Jefferson County, *T. G. Harbison*, October 15, 1914, October 2, 1916, April 15 and May 18, 1917, April 4, 1918 (no. 24), June 24 and 28, 1918 (nos. 34, 35, 37, 40, 41, 42); Choctaw County, *C. Mohr*, August 20, 1880 (no. 55); Blount County, *T. G. Harbison*, October 13, 1906, September 23, 1915; Berlin, Dallas County, *R. S. Cocks*, June 25 and July 28, 1916 (nos. 950, 956).

MISSISSIPPI.—Yazoo City, Yazoo County, *T. G. Harbison*, May 1 and 30, 1915; near Natchez, Adams County, *C. S. Sargent*, April 1913, 1915, and 1916, *Miss C. C. Compton*, April, May, and September 1915; Jackson, Hinds County, *T. C. Harbison*, May 17, 24, and September 18, 1915 (nos. 64, 64a, 78, 78a, 113), *C. S. Sargent*, April 18, 1916; Bolton, Hinds County, *T. G. Harbison*, May 24, 1915.

LOUISIANA.—West Feliciana Parish, *R. S. Cocks*, May 15 and June 12, 1915 (nos. 2528, 2540); near Laurel Hill, *C. S. Sargent*, April 12, 1916; Welch, Beauregard Parish, *E. J. Palmer*, May 17, 1915 (no. 7673); near Opelousas, St. Landry Parish, *C. S. Sargent*, March 17, 1900, April 3, 1913; east of Opelousas, *R. S. Cocks*, April 3 and August 10, 1916 (nos. 4010, 4020); Lake Charles, Calcasieu Parish, *R. S. Cocks*, October 1914, May 21, 1915 (no. 2536), April 3, 1916 (nos. 2530, 4014), *E. J. Palmer*, May 19 and September 11, 1915 (nos. 7695, 8510, 8511); Winnfield quarries, Winn Parish, *R. S. Cocks*, April 18, 1917 (no. 4076); Shreveport, Caddo Parish, *R. S. Cocks*, June 1908 (no. 10), *E. J Palmer*, April 18 and September 6, 1916 (nos. 9479, 10608); sandy hills, Chopin, Natchitoches Parish, *E. J. Palmer*, April 21 and June 12, 1915 (nos. 7342, 7970); sandy upland woods, Natchitoches Parish, *E. J. Palmer*, May 10, 1915 (no. 7574); banks of Red River, Grand Ecore, April 15, 1916 (no. 9449).

TEXAS.—Marshall, Harrison County, *B. F. Bush*, October 8, 1901 (no. 993), *E. J. Palmer*, April 18, June 8, September 26, 1915 (nos. 7279, 8675); Houston, Harris County, *E. J. Palmer*, May 17, September 15, 1915 (nos. 11937, 12763); Livingston, Polk County, *E. J. Palmer*, April 9, 1914 (no. 5151), May 23, 1917 (no. 12003); Pledger, Matagorda County, *E. J. Palmer*, May 8, 1916; Larissa, Cherokee County, *E. J. Palmer*, June 3, September 22, 1915 (nos. 7844, 8619), April 7, September 14 and 16, 1916 (nos. 9373, 9377, 9382, 9387, 10706, 10707, 10709); Groesbeck, Limestone County, *E. J. Palmer*, June 1, 1915 (no. 7833); San Augustine, San Augustine County, *E. J. Palmer*, June 5, 1915 (nos. 7882, 7883), April 19, September 8, 1916 (nos. 9487, 9491, 9498, 10635, 10637), September 9, 10, 1917 (nos. 10730, 12689, 12690); Palestine, Anderson County, *E. J. Palmer*, September 15, 1916, May 29, 1917 (nos. 12085, 12086); Dayton, Liberty County, *E. J. Palmer*, April 3, May 21, 1917 (nos. 11461, 11977); Huntsville, Walker County, *E. J. Palmer*, May 24, 1917 (no. 12024); rocky banks of the Blanco River, Blanco County, April 4, June 5, September 25, 1917 (nos. 11577, 11578, 11579, 11580, 12160, 12164, 12166, 12167, 12171, 12860, 12861, 12866), April 5, 1918 (nos. 13281, 13286); near Boerne, Kendall County, *S. H. Hastings*, June 23, 1911 (no. 201), *E. J. Palmer*, March 27, May 19 and 26, September 27, 1916 (nos. 9265, 9812, 9813, 9823, 9824, 9876, 9879, 9889, 10823, 10824), April 6 and 19, June 13 and 16, September 28–30, 1917 (nos. 11473, 11477, 11485, 11490, 11493, 11594, 11597, 11603, 12239, 12240, 12241, 12243, 12278, 12890, 12897, 12898, 12905); base of the bluff of the Guadalupe River, Kerrville, Kerr County, *E. J. Palmer*, April 8, May 27, June 9, 1917 (nos. 9930, 11503, 12212, 12215, 12216), May 16, 1918 (no. 13269); Lacey's Ranch, near Kerrville, *E. J. Palmer*, May 31, June 6 and 10, July 3, 1916 (nos. 9957, 10032, 12221), April 8, 1917 (no. 11495); rocky banks, upper Seco Creek, Bandera County, *E. J. Palmer*, May 18, 1916 (no. 10236); rocky banks of the Frio River, Concan, Uvalde County, June 14, 1916 (nos. 10183, 10200), April 13, 1917 (nos. 11541, 11542).

ARKANSAS.—Fulton, Hempstead County, *B. F. Bush*, April 11, 1905 (no. 2290), April 28, May 19, June 6 and 10, October 4, 1909 (nos. 5543, 5647B, 5780A, 5814, 5815, 5926), *J. H. Kellogg*, June 20, 1910, *E. J. Palmer*, April 22 and 23, October 19, 1914 (nos. 5355, 5365, 6876), April 10, June 17, 1915 (nos. 7179, 8044), July 18, 1916 (no. 10513); McNab, Hempstead County, *E. J. Palmer*, April 12, June 18, 1915 (nos. 7187, 7204, 8054), April 8, 1916 (no. 9401); Brentwood, Washington County, *E. J. Palmer*, July 7, 1914 (no. 8214); Gum Springs, Clark County, *E. J. Palmer*, June 20, 1915 (no. 8073), July 21, 1916 (nos. 10539, 10543, 10544); Piney, Johnson County, *E. J. Palmer*, June 30, 1915 (no. 8161); Ashdown, Little River County, *E. J. Palmer*, July 21, 1915 (no. 8367); Fort Lynn, Miller County, *E. J. Palmer*, July 19, 1916 (no. 10529); Van Buren, Crawford County, *G. M. Brown*, June 1908; Rogers, Benton County, *B. H. Slavin*, April 30, 1910; Cotter, Marion County, *E. J. Palmer*, September 1, 1915 (no. 804).

OKLAHOMA.—Lenapah, Nowata County, *G. W. Stevens*, August 19, 1913 (no. 2171); near Page, Le Flore County, *G. W. Stevens*, September 8, 1913 (no. 2669), *E. J. Palmer*, October 28, 1915 (no. 9033); Poteau, Le Flore County, *E. J. Palmer*, July 13, 1915 (no. 8281); Fort Towson, Choctaw County, *E. J. Palmer*, July 10, 1915 (no. 8307); Idabelle, McCurtain County, *E. J. Palmer*, July 22, 1915 (no. 8382); Antlers, Pushmataha County, *E. J. Palmer*, July 17, 1915 (no. 8339).

MISSOURI.—Hannibal, Marion County, *J. Davis*, June 5, 1914; Clarksville, Pike County, *J. Davis*, June 16, 1914; Allenton, St. Louis County, *C. S. Sargent*, April 4, 1909; Siebert's Mill, *E. J. Palmer*, August 5, 1916 (no. 10572); Williamsville, Wayne County, *E. J. Palmer*, June 29, 1914 (no. 6126); near Mansfield, Douglas County, *E. J. Palmer*, July 10, 1914 (no. 6254); Elk Springs, McDonald County, *E. J. Palmer*, May 3, 1914 (no. 5473); Galena, Stone County, *E. J. Palmer*, May 20, 1914 (no. 5648), July 25, 1916 (nos. 10561, 10566); Noel, McDonald County, *B. F. Bush*, April 25, October 8, 1909 (nos. 5530, 5983); Eagle Rock, Barry County, *B. F. Bush*, August 10, 1905 (no. 3211), *E. J. Palmer*, July 17, 1914 (no. 6311).

MEXICO.—Coahuila, *Ed. Palmer*, 1880 (no. 118 in Herb. U.S. Nat. Mus.); mountains near Monclova, *Ed. Palmer*, August 19, 1880 (no. 118 in Herb. U.S. Nat. Mus.).

The specimen collected by *Edward Palmer* on the mountains west of Monclova in the state of Coahuila August 19, 1880 (no. 118), and distributed as *T. mexicana* Bentham cannot be distinguished from specimens from western Texas which I have referred to *T. floridana*. *T. mexicana* of BENTHAM (Pl. Hartweg. 35. 1839) is said to have come from the neighborhood of Anganguio in the state of Michoacan in southern Mexico and not to be the same as the earlier *T. mexicana* Schlechtendal (Linnaea 11:37. 1837) collected near Chiconguiaco in the state of Hidalgo, and by HEMSLEY doubtfully referred to *T. americana* Linnaeus. *T. mexicana* Bentham is a nomen nudum.

A variety of this tree which differs only in its glabrous corymbs and puberulous peduncles may be distinguished as

TILIA FLORIDANA var. **australis,** n.var.—*Tilia australis* Small, Flora Southern U.S. 761. 1903; *Tilia pubescens* var. a *Aitonii* f. *glabrata* V. Engler, Monog. Tilia, 129 (in part). 1909.

This variety I have seen only from Blount County, Alabama.

Another linden of this group had best perhaps be considered as a variety of *T. floridana*, distinguished in the shape of its leaves and in their more prominent tufts of axillary hairs. I suggest for the name of this variety

TILIA FLORIDANA var. **oblongifolia,** n.var.—Distinguished from the type by its ovate-oblong leaves with more conspicuous tufts of axillary hairs. Leaves thin, ovate-oblong, long-pointed and acuminate at apex, unsymmetrical and rounded on one side and broadly cuneate on the other, or very oblique and truncate at base, coarsely serrate with apiculate teeth, dark green, smooth and lustrous on the upper surface, glaucescent or pale green on the lower surface, and furnished with usually large conspicuous tufts of axillary hairs, 8–10 cm. long and 6–8 cm. wide; petioles slender, glabrous, 3–4 cm. in length. Flowers 5–6 mm. long, on slender, hoary tomentose pedicels, in wide, thin-branched, stellate-pubescent, mostly 15–20-flowered corymbs; peduncle slender, glabrous, the free portion 2–2.5 cm. long, the bract acuminate at base, rounded at apex, raised on a slender stem, 1.3–1.5 cm. wide, much longer than the peduncle; sepals acuminate, hoary tomentose on the outer surface, villose at the base and along the margins on the inner surface; petals narrow, acuminate, nearly twice as long as the sepals; staminodia narrow spathulate, rounded and erose at apex, about as long as the petals; stigma slightly villose at base. Fruit on slender pubescent pedicels, ellipsoidal, covered with pale brownish tomentum, 6–7 mm. long and 5–6 mm. wide.

A tree with slender, glabrous, pale reddish brown branchlets, becoming dark red-brown in their second year. Winter buds obtuse, glabrous, 4–5 mm. in length. Flowers early in June. Fruit ripens at the end of July.

FLORIDA.—Blue Springs, Jackson County, *T. G. Harbison*, September 18, 1916; River Junction, Gadsden County, *T. G. Harbison*, April 25, 1914 (no. 1478), June 7, 1915 (no. 26); Tallahassee, Leon County, September 12, 1915 (no. 2a); San Mateo, Putnam County, *T. G. Harbison*, June 15, 1915 (no. 2).

ALABAMA.—Bluffs of the Alabama River, near Berlin, Dallas County, *R. S. Cocks*, June 5 and July 25, 1915 (no. 788 type), April and June 1916 (nos. 820, 832, 834, 952, 954, 958), June 3 and 31, 1917 (nos. 1200, 1202, 1204), *C. S. Sargent*, April 19, 1915.

MISSISSIPPI.—Edwards, Hinds County, *T. G. Harbison*, May 18, 1915 (no. 15); near Jackson, Rankin County, *T. G. Harbison*, May 20, 1915 (no. 76); Natchez, Adams County, *C. S. Sargent*, April 17, 1915.

LOUISIANA.—Laurel Hill, West Feliciana Parish, *R. S. Cocks*, March 1910; Avery Island, Iberia Parish, *R. S. Cocks*, May 29 and July 28, 1916 (nos. 4042, 4052); sandy woods, Natchitoches, Natchitoches Parish, *E. J. Palmer*, June 11 and September 27, 1915 (nos. 7956, 8699), April 13 and 14, 1916 (nos. 9416, 9437), June 11 and September 25, 1915 (nos. 7956, 8437, 9416), April 1916, Grand Ecore, May 5, 1915 (no. 7523); Chestnut, *E. J. Palmer*, April 17, 1916 (no. 9462).

ARKANSAS.—Fulton, Hempstead County, *B. F. Bush*, April 11, 1905 (no. 7534 in Herb. Mo. Bot. Gard.); Benton, Saline County, *E. J. Palmer*, June 24 and September 3 and 6, 1915 (nos. 2128, 8129, 8131, 8447, 8479), July 22, 1916 (nos. 10546, 10547, 10548, 10552).

TEXAS.—Marshall, Harris County, *E. J. Palmer*, April 18, June 8 and September 26, 1915 (nos. 7278, 7910, 7913, 8674); Palestine, Anderson County, *E. J. Palmer*, May 29, 1917 (no. 12086); Livingston, Polk County, *E. J. Palmer*, April 3 and May 23, 1917 (nos. 11468, 12003, 12004, 12014).

In *Tilia* a fairly constant specific character can usually be found in the absence or presence of the tufts of hairs in the axils of the leaves, but in *T. floridana* they are usually small and sometimes wanting in what is here considered the typical form of the species from western Louisiana; but westward, especially in Texas and Arkansas, they are usually present and sometimes conspicuous, as they are generally on the leaves of the var. *oblongifolia*, and it is only by the narrower more elongated leaves that this variety can be distinguished. The leaves of *T. floridana* have been described as glaucous on the lower surface, but this is not a constant character, as on the same branch leaves glaucescent and green below often occur. A variety of this species with leaves covered below with a silvery white bloom may be distinguished as

TILIA FLORIDANA var. **hypoleuca,** n.var.

ARKANSAS.—At the foot of a high bluff growing on the rocky margin of White River or on talus sloping to the foot of the bluff in rich soil across the river from Cotter, Marion County, *E. J. Palmer*, June 12, 1914 (no. 5943 type), July 24, 1916 (nos. 10555, 10559).

MISSOURI.—Galena, Stone County, *E. J. Palmer*, October 10, 1913, July 25, 1916 (nos. 4616, 10565); Branson, Taney County, *E. J. Palmer*, June 8, 1914 (no. 5896).

The unusual whiteness of the under surface of some of the leaves of this variety is due to a thick bloom. When this is rubbed off, the surface left is pale green. This bloom appears to be most common on leaves near the ends of branches and is often entirely wanting from those lower down on the branches and from the leaves of young vigorous shoots.

7. **Tilia Cocksii,** n.sp.—Leaves ovate, abruptly acuminate at apex, very oblique at the truncate or rounded base, dentate with small, remote glandular apiculate teeth; when they unfold covered with loose floccose pubescence, nearly glabrous when fully grown early in April; when the flowers open, dark green, and lustrous on the upper surface, pale blue-green and lustrous below, and at midsummer when the fruit ripens, subcoriaceous, dark green and lustrous on the upper surface, paler on the lower surface with slender primary veins without or occasionally with minute axillary tufts, and connected by conspicuous straight or curved veinlets, 9–10 cm. long and 6–7 cm. wide; petioles slender, glabrous, 1.5–2.5 cm. in length; leaves on leading summer branchlets sometimes obliquely cordate, more coarsely serrate, covered on the upper surface with short fascicled hairs, and floccose-pubescent on the lower surface, 10–13 cm. long, 10–12 cm. wide, their petioles puberulous. Flowers 6–7 mm. long, on tomentose pedicels, in compact pubescent many-flowered corymbs; peduncle slender, glabrous, the free portion only 1.5–2 cm. in length, the bract oblong, occasionally slightly obovate, rounded at the ends and sessile, hoary tomentose on the under surface and pubescent on the upper surface when it first appears, and when the flowers open puberulous below and glabrous above, 1.2–1.5 cm. in width and much longer than the peduncle; sepals ovate, acuminate, pale pubescent on the outer surface, villose at the base on the inner surface, a third shorter than the lanceolate acuminate petals; staminodia oblong-obovate, rounded at apex, about half the length of the petals; style glabrous. Fruit globose to depressed-globose, covered with loose brown tomentum, 6–7 mm. in diameter.

A small tree with slender, dull red, glabrous branchlets, the leading branchlets in summer more or less pubescent. Winter buds ovate, acute, dull red, glabrous or pubescent on leading shoots, 5–6 mm. long. Flowers the middle of May. Fruit ripens the middle of July.

Bank of the Calcasieu River, West Lake Charles, Calcasieu Parish, Louisiana, *Sargent* and *Cocks*, March 23, 1917, *R. S. Cocks*, May 15 and July 12, 1918 (no. 4922 type for flowers, 4949 type for fruit); low woods, Lake Charles, Calcasieu Parish, *C. S. Sargent*, March 26, 1911, April 12 and 13, 1915.

From other American lindens *T. Cocksii* differs in the thicker dark green lustrous leaves, in the peculiar bluish color of their lower surface in early spring, and in the pubescence during the summer on the leaves and branchlets of leading shoots in a species which, except when the leaves unfold and the inflorescence first appears in early spring, is otherwise glabrous. It is most closely related to *T. floridana*, from which it differs in the texture, color, and venation of the more finely serrate leaves, in the more compact inflorescence, and in the much shorter free portion of the peduncle. I take much pleasure in associating with this handsome tree the name of Professor REGINALD WOODHOUSE SOMERS COCKS, professor of botany in Tulane University and for many years my companion in annual journeys of exploration through the forests of Louisiana.

ARNOLD ARBORETUM
JAMAICA PLAIN, MASS.

PINE NEEDLES, THEIR SIGNIFICANCE AND HISTORY

JEAN DUFRENOY

(WITH TWENTY-NINE FIGURES)

Are pine needles shoots or leaves? The question may still be debated, since neither the shoot nor the leaf has as yet been clearly defined. A review of the morphology, development, and physiology of the "needles" may be of interest.

Morphology

The definition given by VAN TIEGHEM (**21**), and usually adopted, is as follows: The leaf is symmetrical on both sides of a plane; the shoot is symmetrical around an axis. A needle is symmetrical on both sides of a plane, not around an axis; but by bringing into contact the different needles grouped at the end of a spur shoot, an organ is obtained which is symmetrical around an axis, and which therefore is a shoot. Needles, therefore, are fragmentary shoots. Anatomically they are polystelic shoots which have divided longitudinally into a variable number of parts[1] in order to increase the surface available for carbon assimilation. Being fragmentary shoots, the needle may be considered the homologue of the petiole of broad-leaved gymnosperms. The anatomy of the needle is strikingly similar to that of the petiole in *Ginkgo*, and we may quote COULTER (**4**) as follows: "The most ancient gymnosperms possessed ample fernlike leaves. . . . . The conifers, however, have developed a very different type of leaf . . . . which reaches an extreme expression in small and rigid needles."

The derivation of needles from fernlike phyllodes is apparent from anatomical data.

[1] That the different needles of a spur shoot are parts of the same organ is often strikingly evident. In most cases when a needle bends, the others bend also, so that all can be grouped into a cylindrical, though bent, shoot. When solitary, at the end of a spur shoot, needles are roughly cylindrical in form and shootlike, as normal needles of *P. monophylla*, and abnormal needles of *P. Pumilio* (STRASBURGER), *P. Laricio* (BOODLE **1**), and *P. maritima* (DUFRENOY **13**).

1. RELATION OF PINES TO CYCADS.—"Inverse wood," such as occurs in the petioles of cycads, may be demonstrated on the ventral side of the protoxylem in juvenile leaves and needles of

FIG. 1

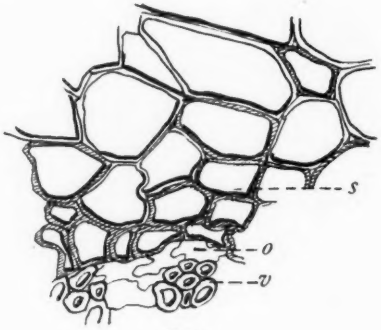

FIG. 2

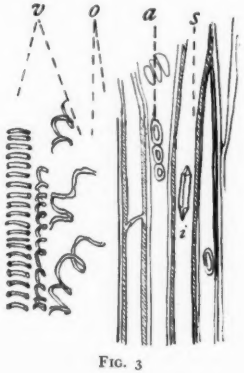

FIG. 3

FIGS. 1–3.—Transfusion sheath in needles of *Pinus maritima** (needle 2 years old, collected May 5, 1918, section 5 mm. above base): fig. 1, part of wood in vascular bundle; *c*, cambium, still dormant; *x*, wood of second year, vessels staining deep red with phloroglucin; *v*, wood of first year (protoxylem), spiral vessels, not staining with phloroglucin; *o*, lacuna; *s*, inverse wood, staining light red with phloroglucin, bright green with methyl green, orange with Sudan III; r^1, resin canal; fig. 2, detail of inverse wood (shaded tissue *s*), showing relation to protoxylem (*v*) and to pitted cells of periderm; *o*, lacuna; fig. 3, longitudinal section of same, showing spiral vessels of protoxylem (*v*) and inverse wood (*s*); *o*, lacuna; *a*, pitted vessels; *i*, oxalate of calcium.

* All the figures are from *Pinus maritima* collected at Arcachon.

P. maritima.[2] In normal needles, however, it is restricted to a few elongated vessels, sparsely distributed among pitted cells, from which they can be easily differentiated. They are always associated with peculiar elongated vessels which stain a bright orange with Sudan III (figs. 1–4). Tumors of **Coccus resinifians,** n. sp.,[3] however, may result in the reversion of the vascular strand in the infected needles to the cycad structure, through the development

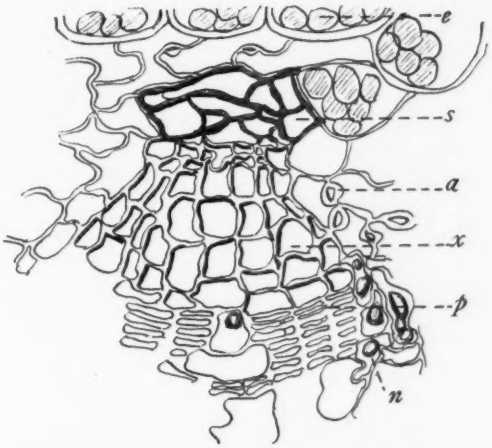

FIG. 4.—Part of periderm of young juvenile leaf (collected May 1918): *p*, phloem, with medullary rays (*n*) crowded with resin drops; *x*, normal wood; *s*, inverse wood in transfusion sheath, staining orange with Sudan III; *e*, endodermis.

of a well defined bundle of inverse wood, which may often extend from the ventral face of the protoxylem to the endodermis (figs. 5–16).[4]

2. RELATION OF PINES TO FERNS.—Other tumor-infected needles show phloem differentiating on the dorsal side of the inverted

[2] VAN TIEGHEM considered the transfusion sheath on the ventral side of normal wood in pine needles to be the homologue of the "inverse wood" in the petiole of cycads. Following TAKEDA (**19**), we found this untenable.

[3] This *Coccus* has been recorded by DUFRENOY from stem tumors of pines, but the name was omitted from the note (**13**).

[4] Stomatal anatomy also emphasizes the origin of cycads and pines from a common stock (REHFOUS **18**).

bundle of xylem, resulting in a fernlike state, comprising two bundles of xylem facing each other, with phloem outside (fig. 7). The relation of pines to the fern stock is further emphasized by the occurrence (in the wood or periderm of tumor needles) of all transitional forms, from normal pitted elements to scalariform cells, such as are present in ferns, and restricted to endodermal cells of normal needles.[5]

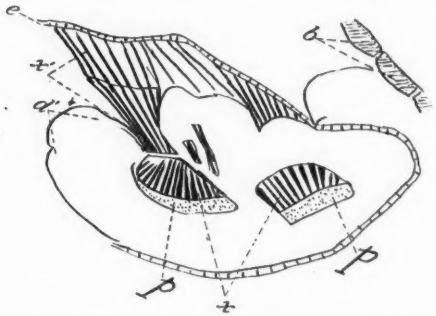

FIG. 5.—Tumor of *Coccus resinifians* on pine needle (collected at Arcachon, dunes of Abatilles, June 1917): part of periderm (schematic); *e*, endodermis, crowded with starch grains (starch and resin are much more abundant in tumor than in sound neighboring tissue); d^1, lignified cells of hyperplasia due to infection by *Coccus; b*, epidermis and hypoderm; *x*, normal wood; *p*, phloem; x^1, inverse wood, composed of sclerenchymatous cells and fibers (staining red with eosin and green with methyl green) and of vessels staining orange with Sudan III; this inverse wood develops from ventral face of protoxylem to endodermis, and is homologous with inverse wood in cycads.

3. RELATION OF PINES TO GNETALES.—Scalariform cells in pine needles may be compared to the tracheae in Gnetales, and suggest the origin of both from a common fern stock.

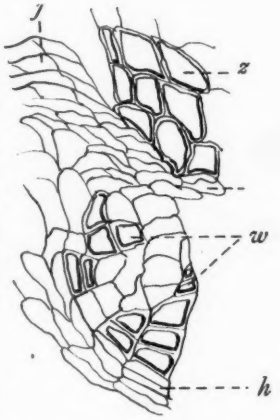

FIG. 6.—Part of fig. 5: *h*, phloem; *w*, lignified vessels in normal wood; *z*, same in inverse wood; *j*, lignified cells with hyperplasia.

4. RELATION OF PINES TO EQUISETALES.—The origin and evolution of the protoxylem is strikingly similar in pine

[5] The perforations in the scalariform cells of pines may be explained as derived from the fusion of enlarged bordered pits, as claimed by THOMSON for Gnetales; but the reverse is probably true, bordered pits being derived from ancestral simple incomplete perforations by acquiring highly specialized characters.

needles and in the stems of *Equisetum*, as it differentiates in both centripetally, from "pôles ligneux," and partially dissolves into lacunae.

The reappearance of polystelic organs, where the stele shows two vascular strands with opposed xylem and peripheral phloem, is fundamental in indicating the origin of conifers from a fern stock. The cycad stele may be derived from the fern stele by suppression of phloem in one of the two vascular strands, the remaining xylem bundle being the so-called "inverted wood." If this inverted wood itself almost entirely disappears, then the normal state of the pine needle is obtained.

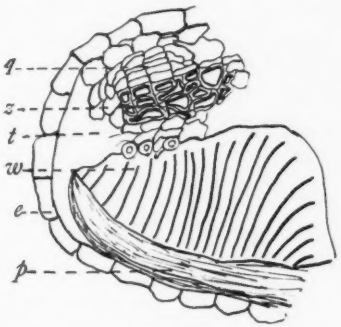

FIG. 7.—Half of vascular strand in tumor needle (collected November 1917): *e*, endodermis; *t*, periderm; *w*, normal wood; *p*, normal phloem; *z*, inverse wood; *q*, phloem.

Development

REJUVENESCENCE AND JUVENILE LEAVES.—Whenever a resting organ grows again, rejuvenescence must take place, and this is always observed in pines, either at the germination of the seed, or when lateral, dormant buds are caused to develop pathologically. When the pine seed germinates, cotyledons develop on the young shoot, and then single juvenile leaves. These are smaller the higher up the shoot they develop, and at a certain height they are mere scale leaves. It is at the base of

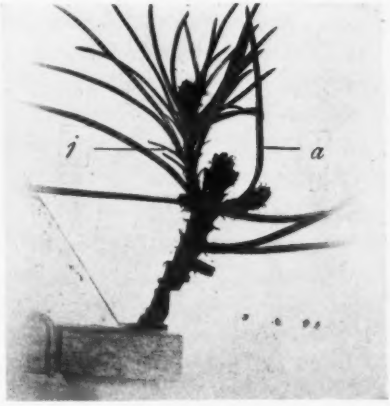

FIG. 8.—Proliferating spur shoots, springing up between the two geminate needles (*a*); *j*, juvenile leaf with spur shoot in axil.

these scales that the spur shoot of the needles arises. After it has developed a few scale leaves and a tuft of needles, this spur shoot generally remains dormant. If, however, the terminal bud of a branch happens to die, these lateral shoots may grow into a normal branch, bearing at first isolated juvenile green leaves and then scale leaves with spur shoots in their axils (fig. 8).

VARIATIONS IN THE NUMBER OF NEEDLES.—The number of needles on the spur shoot of each species is considered constant enough to be used as a character for classification; still, on rejuvenated or infected twigs, shoots are found which bear an unusual number of needles. BOODLE (1) makes the following statement: "In *Pinus monophylla* the spur shoots as a rule bear each a single needle, but two are occasionally present. MASTERS found by studying early stages that two leaf rudiments are always produced, but that one of them generally becomes arrested at an early stage."

Single needles have been observed by BOODLE on *P. Laricio*, and we found some on twigs of *P. maritima* that were infected by the larva of a xylophage insect (*Hylesinus piniperda*). These single needles are roughly cylindrical; in many cases a groove is present on one side of the leaf. On following it downward, it is found to contain two papillae, one of which is the apex of the spur shoot, the other the rudiment of the second needle. Variation in the number of needles in this case is due to arrest in the development of one of them. It is a rare occurrence in *P. maritima* and *P. Laricio*, but it has become the rule in *P. monophylla*. The multiplication of needles on the spur shoot has often been recorded on wounded, infected (13), or vigorous (20) shoots, and it has been regarded as a reversion toward ancestral, many-leaved gymnosperms (3).

Although these variations are somatic in origin, we have proved that they comply with Mendel's law, in that the proportion of bud mutations on the shoot is precisely that of F_2 recessives in the case of hybrids. Shoots of vigorous *P. maritima* or those infected with *Coccus resinifians* have been observed to yield 75 per cent normal 2-needled spur shoots, and 25 per cent 3-needled spur shoots. Proliferating spur shoots on *P. virginica* in Arcachon often yield 75 per cent normal 3-needled spur shoots, and 25 per cent abnormal

2-needled spur shoots, or vice versa (**14**). These bud mutations, like proliferating spur shoots,[6] are due to modifications in the normal nutrition of the pine, caused by environmental factors, traumatisms, and chiefly parasites, and they result in increase of osmotic pressure in differentiating tissues.

That osmotic pressure is the ultimate determining factor is demonstrated by the fact that we were able to force 7-year old *P. maritima* to produce 3-needled spur shoots or proliferating spur shoots by watering abundantly, which of course increased tur-

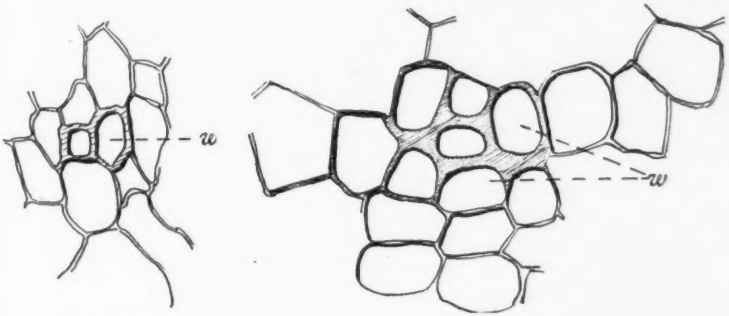

FIG. 9 FIG. 10

FIGS. 9–10.—Fig. 9, protoxylem in first needle appearing on juvenile pine: *w*, cells whose walls begin to show lignification and stain red with phloroglucin; fig. 10, protoxylem in very young needle of juvenile pine: section near apex; only one xylem pole.

gescence of cells. Whether needles or juvenile leaves develop depends upon the relative supply of soluble osmotic material to the cells. Needles, or all adult organs in general, develop from material obtained from the earth and atmosphere, by gradual assimilation. Juvenile leaves, or all juvenile organs in general, develop from material stored in the reserve tissue (**9**).

TRANSITION FROM JUVENILE LEAVES TO NEEDLES.—As needles and juvenile leaves are but different responses of the same organism to environmental factors, they may be assumed to show transitional

[6] Development of lateral long shoots is exaggerated on pine seedlings exposed to sea wind, and results in "buissornement," like that recorded by DEVAUX (**6**) for *Erica* on ocean dunes.

forms (contrary to the opinion of DAGUILLON 5). In fact, transitions are observed. The first needle to appear on juvenile pines shows anatomical features of juvenile leaves (figs. 9–17); and

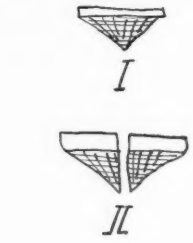

FIG. 11

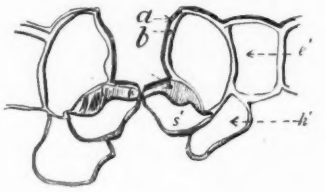

FIG. 12

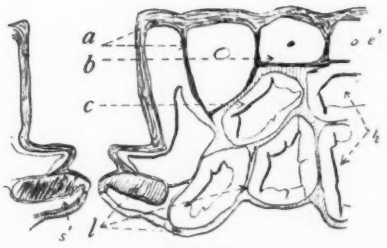

FIG. 13

FIGS. 11–13.—Fig. 11, transition from one vascular bundle to two semi-bundles in successive transverse sections from apex to base of needle: primary wood at apex (I) grouped into one bundle and like wood in juvenile leaves or in leaves of ancestral gymnosperms; with secondary structure, wood divides into two fragmentary bundles and becomes more like that in shoot (II–IV); fig. 12, stomatal cells of first needle produced on juvenile pine, showing structure of stomatal cells in juvenile leaves: no hypodermal cell present except below stomatal cells; letters as in fig. 13; fig. 13, stomatal and epidermal cells of needle on adult pine: *a*, cutin, staining orange with Sudan III; *l*, lignin, staining red with phloroglucin; *b*, thickening of epidermal cells, staining green with cotton blue; *c*, thickening of hypodermal cells; *h*, hypoderm; e^1, epidermis; s^1, stomatal cell (note local thinning of lignified wall, forming hinges).

transitions from one vascular bundle (as shown in juvenile leaves) to two semi-bundles (as typical of needles) is observed in successive sections of needles from the apex downward (fig. 11).[7] Needles

[7] The anatomy of needles varies so much from apex to base as to make all comparison worthless unless distance of the transverse section from the apex be clearly stated. The same statement applies to the age of the needle and the season when material is collected.

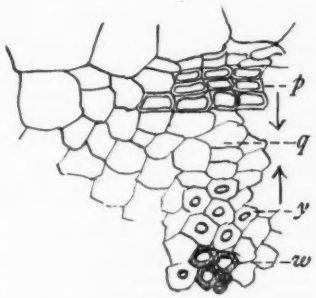

FIG. 14

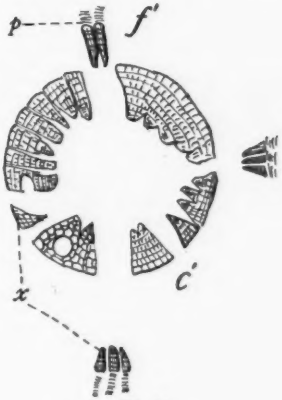

FIG. 15

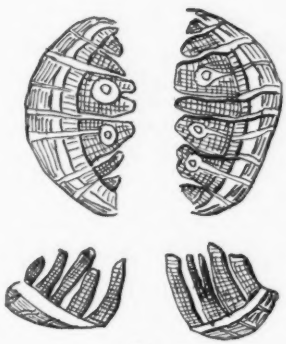

FIG. 16

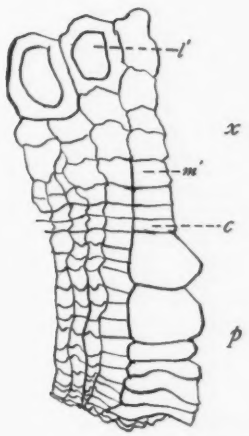

FIG. 17

FIGS. 14–17.—Fig. 14, periderm of very young juvenile leaf (collected April 25, 1918): *w*, protoxylem; *p*, phloem; *y*, cells of future wood beginning to lignify; *q*, procambium; arrows indicate direction of differentiation; wood first differentiates centripetally and procambium becomes more narrow until finally it is a mere band of cambial cells; note identity of procambium in juvenile leaves and in first needles of juvenile pines (cf. *w*, figs. 9 and 10); fig. 15, course of vascular bundles in shoot of juvenile pine bearing juvenile leaves: c^1, cauline vascular bundles; f^1, foliar vascular bundles; *x*, xylem; *p*, phloem; fig. 16, course of vascular bundles in proliferating spur shoot: xylem inside (crossed lines), phloem outside, and cambium between, also resin canals and medullary rays; f^1, foliar bundle consisting of 2 semi-bundles each divided by well defined medullary rays; fig. 17, part of foliar bundle (f^1) in needle of proliferating spur shoot (collected May 3, 1918), part of f^1 of fig. 16: *c*, cambium active and producing spring wood above (*x*) and phloem (*p*) below; l^1, wood vessels; m^1, medullary rays; note that revegetation begins sooner in proliferating shoots than in normal spur shoots, which are still dormant at this season (cf. fig. 1).

may also be derived from juvenile leaves through such transitional forms as bilobed juvenile leaves (figs. 18–20) and concrescent needles[8] (fig. 21).

FIG. 18.—Proliferating shoot bearing double (bilobed) juvenile leaves.

Histology

The chemical nature of the cell walls may afford good data for the comparison of pine needles with juvenile leaves or with phyllodes of other gymnosperms, living and fossil. Pine needles appear to be more differentiated histologically than morphologically, 18 tissues being recognized from color reactions (see table I).

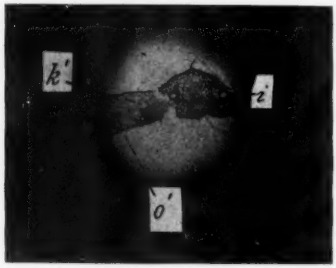

FIG. 19.—Transverse section of double juvenile leaf along plane *ab* of fig. 18; o^1, double vascular bundles; k^1, intraparenchymatous resin canals such as usually occur only in needles; *i*, hypodermal resin canal typical of juvenile leaf; microphotograph, obj. 3.

Physiology

Living cells must excrete poisonous materials which result from the disassimilation process (12). In the cells of pines these materials are resinous drops, which must be gotten rid of. In the primitive organs, resin probably filtered through the epidermis, and the epidermal cells were also secreting cells. This is still the

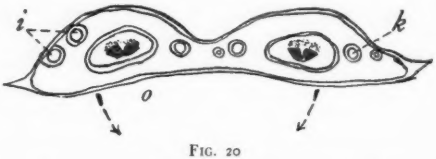

FIG. 20

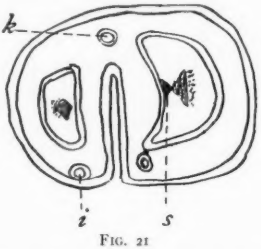

FIG. 21

FIGS. 20–21.—Fig. 20, schematic view of fig. 19: note that each vascular strand contains 2 semi-bundles, as in typical needles; fig. 21, concrescent or double needle: note hypodermal resin canals such as are typical of juvenile leaves, also inverse wood (*s*) on ventral side of protoxylem.

[8] These concrescent needles have been considered the homologue of the double needles of *Sciadopitys*. They may be homologized with bilobed juvenile leaves bent as shown by arrows in fig. 20.

TABLE I

Histology of adult pine needle	Gentian violet	Methylen blue	Methyl green	Cotton blue*	Sudan III†	Phloroglucin	Devaux's method for pectose‡	Safranin in solution of ferrous chloride	HCl vapors
Cuticle					orange red				
Epidermis: Middle lamella	red	deep blue			orange	red			
Thickening	light violet			green				red	
Hypoderm: Middle lamella	red	deep blue		deep blue		red	blue	red	rose
Thickening	light violet			light blue			blue	red	
Mesophyll								yellow	
Transverse walls of endodermis			deep green			red		red	
Fibers around resin canals							blue		
Periderm		light blue						light rose	rose
Transfusion sheath (inverse wood)					bright orange	light red		red	
Protoxylem (spiral vessels)							blue	rose	
Metaxylem	red	deep blue	green	blue		deep red		deep red	rose
Phloem	violet			blue			blue de Prusse	yellow	
Sclerenchymatous fibers	red								
Cicatricial periderm in cankers					light orange	light red			
Resin drops				blue	orange or yellow				

* Lactophenol solution. † Alcohol and glycerine solution. ‡ Sections stained in ferrous chloride, then washed in distilled water, and treated with ferrocyanide of potassium +HCl; pectose stain "blue de Prusse" (2).

case for the stamens and scales of pines, in which resin is excreted from the epidermal secreting cells. In juvenile leaves most epidermal cells become sclerenchymatous (to protect the parenchyma), and a very few still secrete resin (figs. 22, 23). Internal organs then differentiate, which can store resin, so that parenchymatous cells do not get poisoned, and resin canals run from the needles to the shoot and into the roots. The possibility of getting

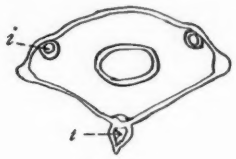

FIG. 22

FIG. 23

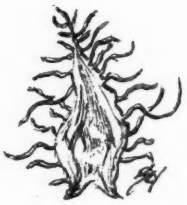

FIG. 24

FIG. 25

FIG. 26

FIGS. 22–26.—Fig. 22, abnormal juvenile leaf showing secretory hair (*t*) on ventral face; fig. 23, abnormal needles showing rudimentary secretory hair (*t*) on ventral face; fig. 24, scale leaf: strikingly similar to scale of *Cycas;* the hairs may be interpreted as sterilized ancestral ovules or stamens: fig. 25, juvenile leaf, showing hairs that may be interpreted as ancestral stamens, now sterile and secretory; fig. 26, secretory hairs of scale leaf (left) and juvenile leaf (right): *s*, secretory hair; *e*, epidermal cell.

rid of refuse poisonous material probably explains why coniferous trees are evergreen, whereas most of the other trees periodically lose their leaves and rest in winter.

Pathology

The needles of *Pinus maritima* may last 5 or 6 years. Often their death must be due to an accident, either a general trouble in the nutrition of the tree, or a local infection by rust or smut.

In the piñadas of Gascony, many of the needles which are infected in early spring by the aecidium of *Coloesporium senecionis* (*Peridermium oblongisporum* Kleb.) dry up and fall in summer. The "maladie du rouge" is very prevalent and the most important cause of the falling of needles, bringing ruin to many pine nurseries. It derives its name from the red patches that appear and spread on infected needles. It is due to several species of Asco-

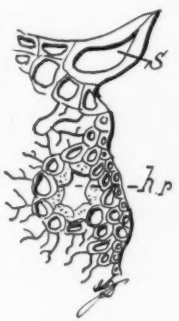

FIG. 27

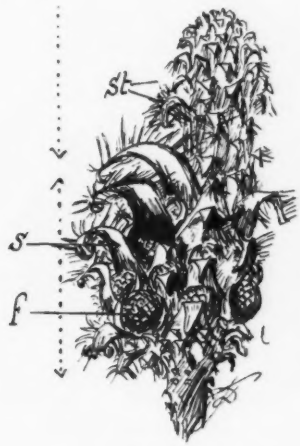

FIG. 28

FIGS. 27–28.—Fig. 27, transverse section of juvenile leaf: *s*, secretory hair; *hr*, hypodermal resin canal; fig. 28, staminate cone of *P. maritima:* basal part, protected from sea wind by ridge in dune, normal and fertile (*s*, scale; *f*, flowers); upper part, exposed to sea wind, sterilized; collected on sand dunes of Arcachon, May 1917; note gradual reduction and sterilization of flowers from base upward.

mycetes: *Lophodermium pinastri*, which is the most common on several species of pine (*P. sylvestris, P. Pinea, P. maritima*); *Hypoderma pinastri*, the conidial form of which was observed by DUFRENOY on *P. maritima;* and *H. strobicola*, observed by FRON on *P. Strobus*.

Conclusion

Morphological variations are but the result of physiological variations (9). The different forms of the different phyllodes of pines, juvenile leaves, scale leaves, fertile leaves (♂ and ♀ flowers),

and assimilatory organs (needles) differ widely; but abnormal transitory forms (figs. 24–28) which we have observed and described in previous works (**9**) allow us to state that all the forms of the different organs of pines are but different distorted features of a unique ancestral organ which, like the gametophyte of ferns, possessed at the same time the three different physiological functions of reproduction, assimilation, and protection (**10, 11**).

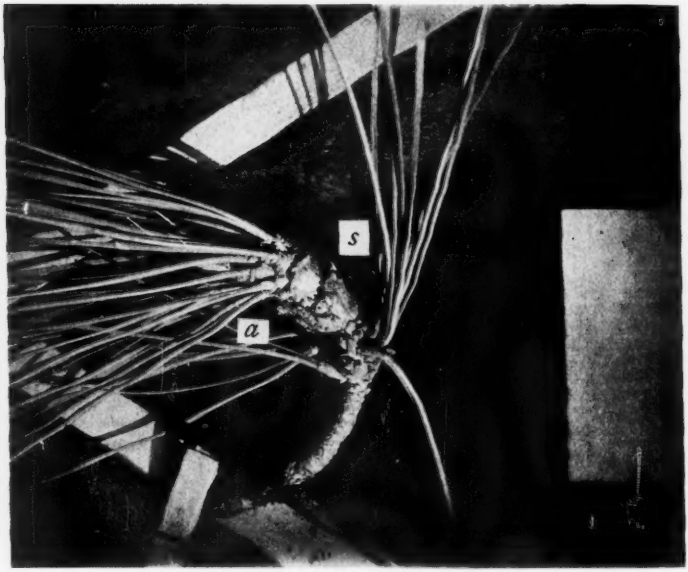

FIG. 29.—Photograph of ♂ inflorescence of *P. maritima*, shoot bent by sea wind; *s*, sterile scales on upper exposed side, with rudimentary ♀ flowers developing at base of scale in place of normal ♂ flowers; *a*, normal ♂ flowers on protected side; sterilization is gradual from protected to exposed flowers.

All the phyllodes of the primitive coniferous trees were probably fertile, and like the fertile leaf in *Cycas*, but under the pressure of unfavorable ecological conditions some parts became sterile scales. This is not mere formal hypothesis; such a sterilization has actually been observed. On the dunes of Gascony, for instance, the parts of the male flowers which are exposed to sea wind are sterilized (fig. 29), and scales develop in the place of stamens (**8**).

In like manner all the different organs must have descended from the ancestral organ; each lost the possibilities corresponding to the function it lost, but retained and perfected those which made it more adequately adapted to its special function. The following table shows how the different organs of pines may be derived from one another, according to data given by studies of abnormal, intermediate forms at the Biological Station of Arcachon.

Primitive organ
- fertile (reproduction)
  - ♂ fertile leaf
  - ♀ fertile leaf
- green (assimilation) → juvenile leaf
  - shoot
  - needle
- storage of reserves → cotyledonary needle (7)
- self-protecting → scale

A needle which has specialized in the assimilation of carbon is itself a sort of assimilating organ; leaves of angiosperms are another.

Needles are the physiological leaves of pines. They differ from leaves in that they are perennial and are much less fragile. Typical leaves are temporary, delicate, perfectly shaped for intense assimilation, but unable to stand bad weather. Pine needles last several seasons. They have efficient xerophytic adaptation and can stand the roughest weather on arid lands, windy mountain tops, or storm beaten coasts (**15, 16, 17**).

In conclusion, thanks are extended to Professor FRON for his valuable encouragement, and to Dr. F. LALESQUE, Honorary President of the Station Biologique d'Arcachon, for his many kindnesses and valuable documents.[9]

STATION BIOLOGIQUE D'ARCACHON

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[9] We are also indebted to The Bureau of Plant Industry, Professor R. T. BAKER, Dr. FRAGOSO, and Professors GUILLIERMOND and MAIRE for most valuable papers; while part of the expenses involved in these researches was defrayed by a grant from the Association Francaise pour l'Avancement des Sciences.

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BRIEFER ARTICLES

JOSEPH YOUNG BERGEN

(WITH PORTRAIT)

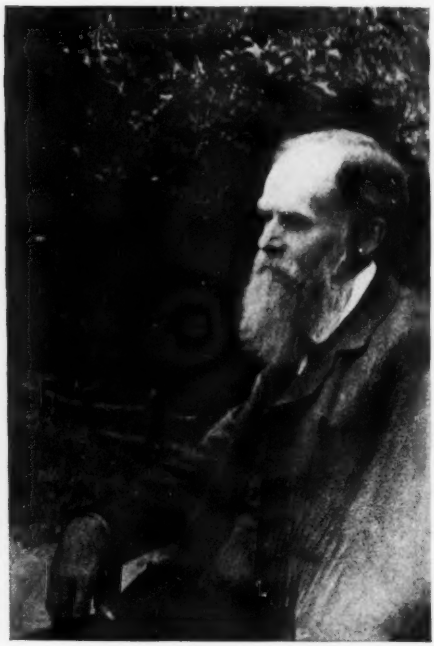
There are many ways of advancing science, and hardly less significant than the investigator is he who makes men wish to investigate. Unquestionably no small number of those who have advanced botany have come to it with an inclination formed before university days, and he who set their compass was often one of those wise enthusiasts who guided their first steps in science.

If we should take into account this service alone, American botany would acknowledge its debt to JOSEPH YOUNG BERGEN, who died at his home in Cambridge, Massachusetts, on October 10, 1917. He was born February 22, 1851, at Rye Beach, Maine, his family moving in 1855 to Peoria, Illinois, where for some years the family home was beautifully situated on the bluffs outside the city. Here the nature-loving parents were accustomed to take their children on pleasant country trips to gather flowers, fruits, or nuts, according to the season. This home influence was strengthened for our future botanist by an intimate acquaintance with Dr. STEWARD, an old-time physician of Peoria, who took the lad on many of his professional drives into the surrounding country. This amateur botanist watched the progress of growing things along the roadside, and new or especially interesting plants found their way into the doctor's buggy for more careful inspection at his leisure.

Although the boy was prepared for college chiefly by home study, he had some time in the grammar and high schools in Peoria and two years in the old academy at Pembroke, New Hampshire. In due course he went to Antioch College in southern Ohio, that small but memorable institution whose first president was HORACE MANN, of well known influence in the educational world. It is probable that at Antioch he received that bent toward geology which led to his first scientific work, done in connection with the Ohio State Geological Survey. Later he made practical application of his geological and chemical training in dealing with the problems of lead and zinc mining at Joplin, Missouri.

In 1876 he married FANNY DICKERSON, also of Antioch College, in collaboration with whom in 1890 he published "A Primer of Darwinism and Organic Evolution." Mrs. BERGEN'S interests turned later to American folk lore, to which she has made a significant contribution.

In 1878, not long after his marriage, Mr. BERGEN returned to New England and began his long career as a teacher by becoming principal of the high school at Deerfield, Massachusetts. Three years later he accepted an appointment as professor of the physical and biological sciences at Lombard College, a position which he relinquished after 2 years. In 1887 he became teacher of physics in the Boston Latin school. Physics as taught in the high schools of the time was more often an exercise in textbook study than one of application of principles to laboratory practice. Doubtless to one of Mr. BERGEN'S broad experience and keen perception of real values the lack of adequate presentation came home with unusual force. In 1891, in collaboration with Professor E. M. HALL of Harvard University, Mr. BERGEN brought out the well known textbook in high school physics which had a far-reaching and permanent influence on the teaching of this science in America. Although his chief interest was later transferred to botany, he maintained an active connection with the teaching of physics by acting for 10 years as instructor in this branch in the Harvard summer school.



In 1889 Mr. BERGEN went to the Boston English high school as a teacher in biology, where he remained for 12 years, during the remainder of his career as a teacher. Here again the need of a new presentation

of his subject for high school work led to the writing of his "Elements of Botany" in 1896. The practicable way in which the main features of the newer botany with its greater emphasis on the physiological aspects of the subject were brought out in text instruction and directions for laboratory study went far to make the book an important influence in turning botanical instruction in secondary schools away from the rather dry descriptions of form, to the more interesting and equally valuable study of the activities of life. This book and its successors, the "Foundations of Botany" (1901) with keys to the commoner plants of the great divisions of the country prepared by Miss ALICE EASTWOOD, Professor S. M. TRACY, and by himself, the "Principles of Botany" written in collaboration with Dr. BRADLEY M. DAVIS in 1906, "Essentials of Botany" (1908), "Practical Botany" in collaboration with Dr. OTIS W. CALDWELL in 1911, and "Introduction to Botany" by the same authors in 1914, have provided a series of elementary texts which have kept abreast of the newer movements in botanical development and have served to induct a vast host of young Americans into the study of plants. The success of these books brings sufficient evidence of a wise choice of material and of clearness and adequacy of presentation.

While Mr. BERGEN is perhaps most widely known as a teacher and writer of books, he was also a genuine investigator. Both by early training and by inclination a man of out-of-doors, he found his instincts for the field leading him toward the problems of ecology, and his perhaps equally strong inclination toward the precision of the laboratory investigator led him when opportunity presented itself to a fruitful application of laboratory methods to the study of plants in their environment. His opportunity came when in 1901 he retired from teaching and went to southern Italy, where in the neighborhood of Naples he spent some 4 years. Here he made use of the rich facilities of the Biological Station and made the valued acquaintance of FEDERICO DELPINO, Professor of Botany at Naples University, and of other members of the botanical faculty. He found great delight in tramping with Professor MATTEI, now of Palermo, who at that time was mapping the flora on the Solfatara, the partially active volcano near Pozzuoli. After a midday dinner at the Bergen residence they would "tramp off over that wonderful phlegrain plain, perhaps through a basaltic paved Greek lane, perhaps passing some wonderful ruined Greek temple or haunt of Horace or Virgil on their way out into the country." The results of this happy time found their way to the botanical world chiefly through short articles printed in the BOTANICAL GAZETTE and in *Plant*

World between 1903 and 1909. The transpiration problems of the xerophytes of the Neapolitan region, drought tolerance, reactions to light, and the behavior of strand halophytes were among the subjects dealt with in at least a dozen articles. One article on his friend DELPINO (Science **21**:996) recalls the personal relations of those days.

Of course to one whose life had been given largely to teaching, pedagogical matters would necessarily present their claim, and here Mr. BERGEN'S broad experience and sympathetic common sense always contributed genuine substance to the discussion. After his return to Cambridge from Italy, Mr. BERGEN'S time was for the most part spent on his series of textbooks.

Although Mr. BERGEN took but little part in the work of scientific societies, the circle of botanists and zoölogists who in their Cambridge days found the Bergen home a place of sincere hospitality and of helpful appreciation and encouragement would of itself form a very respectable society. The direct searching comment, the enthusiastic cheering-on, and the sympathetic and straightforward honesty met there were tonic and corrective and stimulant all in one. There are many of us who feel that we owe him a never-to-be-forgotten debt for these and for still more precious gifts.

I am permitted to add an incident told immediately after Mr. BERGEN'S death by the gentleman to whom it happened. A few years ago a western botanist, visiting the Harvard Botanic Garden, noticed a tall, spare man of distinguished appearance deeply absorbed in some observations he was making among the flower beds. The visitor asked one of the old gardeners near by if he could tell him the gentleman's name. The old man replied "We call him Saint Joseph."

I believe that in every one of the wide circle of those who called Mr. BERGEN friend this incident will find an echo. In remembering him we value the botanist and the teacher, we respect the far-reaching penetration and creative work of the scientist, and we acknowledge and revere the rigor, the force and moral fervor, the patience and exceeding gentleness of the saint.—RODNEY H. TRUE, *Bureau of Plant Industry, Washington, D.C.*

CURRENT LITERATURE

NOTES FOR STUDENTS

Development in gymnocarpous Agaricaceae.—In a recent paper Miss DOUGLAS[1] describes the development of 7 species of gymnocarpous Agaricaceae. She studied one species of *Mycena* (*M. subalcalina*), 3 of *Hygrophorus* (*H. miniatus*, *H. nitidus*, and *H. borealis*), and 3 of *Entoloma* (*E. flavifolium*, *E. grayanum*, and *E. cuspidatum*). The general course of development is alike in all the species, the variations presented relating to specific or generic features. The fundament of the fruit body just before the differentiation of the stipe and pileus primordia is cone-shaped, homogeneous in structure, the hyphae more or less interlaced and branched, extending in general parallel with the central axis of the cone. The surface is more or less floccose from the ends of single hyphae, or minute tufts, which diverge slightly. The young fundament of *Entoloma cuspidatum* differs from that of the others in being greatly elongated in proportion to its diameter, being nearly cylindrical, or even slightly clavate, with a conoid apex. The slender, elongate fundament appears to bear a direct relation to the slender form of the mature basidiocarp, and also to the very moist habitat of the species. The specimens studied were growing in sphagnum. The rapid elongation of the fundament serves to bring the growing points out of the watery environment in which they originate at the apex of slender rhizomorphs.

The growing point for the formation of new tissue is apical, while elongation occurs in the older hyphae. The first evidence of pileus formation is a great increase in the apical hyphae which begin to diverge, thus giving to the young fundament a sheaflike form. The pileus and stipe fundaments are thus differentiated. While apical growth of the basidiocarp continues, the most active seat of new tissue formation is now shifted from the apex to the annual furrow between pileus and stem primordia, and later to the under surface and extreme margin of the pileus. This marks the origin of the hymenophore. It begins at once in the 3 species of *Hygrophorus*, but is delayed for a short time after differentiation of the stipe and pileus fundaments in *Mycena subalcalina* and in the 3 species of *Entoloma*. It is recognized by the rich protoplasmic content of the hyphae, which usually react more strongly to stains, and thus become more deeply colored. The growth direction of these hyphae of the

[1] DOUGLAS, GERTRUDE E., The development of some exogenous species of agarics. Amer. Jour. Bot. 5:36–54. *pls. 1–7*. 1918.

hymenophore primordium is perpendicular to the point of their origin, whether over the upper end of the stem, in the angle between stem and pileus, or on the undersurface of the pileus. Their course is parallel, although in the angle of the furrow there is more or less of a convergence in their growth direction. At first these hyphae are very slender and terete, but later they become stouter and blunt. From the time of their origin they form a palisade layer whose surface is, in general, level until gill formation begins. In the majority of the species, the ends of the hyphae soon reach the same level. Their "register" is even, and the surface compact; but in *Hygrophorus miniatus* and *H. nitidus* the palisade for some time is not compact and the hyphae do not register evenly. The even register of the palisade hyphae is delayed in these species for some time after the origin of the gill salients.

During the early stages of development of the hymenophore there is a strong epinastic growth of the pileus margin, causing it to curve downward and inward. This is particularly strong in most of the species, less so in *Entoloma cuspidatum* and less so in *Hygrophorus nitidus*. The gill salients are formed by the more rapid downward growth and extension of the subjacent tissue in regularly spaced radial areas. The development advances in a peripheral direction from the stem toward the margin of the pileus. The growth direction is perpendicular to the morphological undersurface of the pileus, and the situation from this standpoint can readily be understood when the pileus margin is strongly incurved.

In the palisade layer, which eventually becomes the hymenium, the elements are multiplied by branching of the subhymenial elements. In the species of *Hygrophorus* in particular, and to some extent also in *Entoloma flavifolium*, the pressure of the increasing palisade loosens up the elements of the subhymenium, and this is evident as a zone of less density. This peculiarity is well shown also in *Omphalia chrysophylla* and *Clitocybe cerussata* studied by BLIZZARD.[2]

In both these papers dealing with gymnocarpous forms, it is shown that the origin and the general course of development of the hymenophore corresponds with that of angiocarpous forms of the *Agaricus* type. It is further shown that there is a tendency in the early stages of development for a superficial zone of the pileus, here of quite limited extent, to be arrested in growth, sometimes quite regularly and normally. The regular course of development being thus shifted to a slightly interior zone presages the later evolutionary type of development presented by the angiocarpous forms, where the origin and differentiation of stipe and pileus primordia are shifted permanently to the interior of the young basidiocarp primordium, with a more or less well marked external zone, the blematogen.—GEO. F. ATKINSON.

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[2] BLIZZARD, A. W., The development of some species of agarics. Amer. Jour. Bot. 4:221–240. *pls. 6–11.* 1917.

Self-sterility.—EAST and PARK[3] have recently published the results of some extensive experiments on 4 self-sterile species of *Nicotiana*, and have proposed an explanation. In the past there have been several attempts to interpret self-sterility as a response to environmental factors, notably humidity. Such interpretations may have been quite true in some cases of self-sterility, where only a single race of plants has been involved, but highly unsatisfactory in explaining cases where pollen fails on own stigmas and functions on stigmas of another race. It is such a situation that the authors have dealt with, and they have shown conclusively for their material that self-sterility is inherited. Normal seasonal changes at times induced "pseudo self-fertility" in their self-sterile races, but "other environmental factors appeared to have little or no influence on self-fertility."

As to the physiological nature of self-sterility, the authors state that it is involved with rate of pollen tube growth. This in itself suggests that self-sterility behaves as a sporophytic character. The fact is more definitely demonstrated, however, "by the behavior of reciprocal matings, pairs of reciprocals always giving like results either when fertile or sterile."

Going further, the authors state "that modern discoveries tend more and more to show that the sole function of the gametophyte of the angiosperms is to produce sporophytes. The characters which they possess appear to be wholly sporophytic, the factors which they carry functioning only *after* fertilization." This statement seems directed at such theories as that of BELLING, who has given us a striking explanation of "semi-sterility" in beans, on the basis of the direct influence of the germinal equipment of gametophytes upon the gametophytes themselves. It is quite probable, however, that the two cases are involved with distinctly different phenomena, since BELLING'S material showed degeneration and sometimes complete abortion in pollen and embryo sacs, while the Nicotianas of EAST and PARK were self-sterile merely because of the failure of pollen tubes. The hereditary mechanism of the two cases must be quite different.

To explain the hereditary behavior of their Nicotianas, the authors have assumed a mechanism involving multiple allelomorphs and crossing over. If two plants differ in but one of a number of effective factors, they are fertile in intercrosses. "Intrasterile classes" are composed of individuals which differ in none of the effective factors. Anything like a thorough appreciation of this theory can be obtained only from the original article.

This explanation seems sufficiently accurate in interpreting the results of the authors, as well as the results of some of the earlier investigators. From a practical point of view, however, it seems rather unsatisfactory, since it considers only the behavior of self-sterile plants when bred *inter se*. The authors

[3] EAST, E. M., and PARK, J. B., Studies on self-sterility. I. The behavior of self-sterile plants. Genetics **2**:525–609. 1917.

state that "all questions connected with the relation between true self-fertility and self-sterility have been omitted designedly as pertaining to a distinct problem." Are we unreasonable in asking for a single theory to explain both self-fertility and self-sterility? Are we wrong in thinking that the significance of self-sterility lies in its relation to self-fertility? Such a general theory, no doubt, will be provided by the authors in their later reports; the present publication evidently represents merely the first of a series on the general subject of self-sterility.

The explanation also has another theoretical shortcoming, similar to that which applied to EAST's "heterozygosis." In heterozygosis EAST stated that hybrids are vigorous because of their heterozygous sets. This virtually amounted to saying that hybrids are vigorous because they are hybrids. "Heterozygosis" was a more accurate and scientific statement of the fact of hybrid vigor, but it was not an explanation. Now EAST states that pollen will not function on stigmas of a plant of which the germinal constitution is the same as that of the plant which produced the pollen. Couched in a terminology involving multiple allelomorphs and crossing over, this may well be a more accurate and scientific statement of the facts of self-sterility and its behavior in inheritance, but it is not an explanation. Such scientific restatements are very valuable in helping to organize facts, and "heterozygosis" unquestionably had such a value. The present theory, however, seems at first sight a much less valuable one, since it is so elastic as to be confusing.

But whether the theoretical argument of the authors is destined to stand or fall, they have done an exemplary piece of research. This seems to have been the first satisfactory experimental attack upon the problem of self-sterility, and the resulting data are therefore extremely valuable.—MERLE C. COULTER.

Buffer processes in succulents.—JENNY HEMPEL[4] has made a very important addition to our rather limited knowledge of actual reaction in plants. Succulents were used in this work, since, with their well known wide and rapid variations in acid content, they might be expected to supply especially interesting material for such a study. Determinations by the use of the hydrogen electrode were made on the juices of numerous specimens of the plants studied, after they had been exposed to varying conditions. The values found range from $P_H = 3.9$ to $P_H = 5.7$. Higher acidity than the more acid of these values is recorded in the same work in lemon juice ($P_H = 2.19$); and by HAAS[5] in citrus fruits ($P_H = 2.22$–3.8), in cranberries ($P_H = 2.4$), and by a less exact method[6] in the petals of certain flowers (P_H = about 3).

[4] HEMPEL, JENNY, Buffer processes in the metabolism of succulent plants. Compt. Rend. Trav. Lab. Carlsberg **13**:1–129. 1917.

[5] HAAS, A. R. The reaction of plant protoplasm. BOT. GAZ. **63**:232–235. 1917.

[6] ———, The acidity of plant cells as shown by natural indicators. Jour. Biol. Chem. **27**:233–241. 1916.

It would seem that such marked changes as were found in the reaction of the juices of active tissue must affect considerably the metabolic processes, as well as the physical condition of the tissue. CROCKER[7] has suggested that these changes may be important in the regulation of transpiration by succulents. The lower values are of the same order as those reported in the same work by HEMPEL and also quoted from WAGNER for non-succulent plants. Such P_H values range from 5.4 to somewhat above 6. Slightly alkaline juices are reported by HAAS (*loc cit.*) in the petals of certain flowers; he finds, however, that blue pigments by no means always indicate an alkaline reaction.

As the title suggests, the principal object of the work was to gain some information as to the substances in the plant juices which act as buffers, or regulators of their reaction. On the acid side of the neutral point the following data were obtained for this study: (1) titration to the litmus end point ($P_H = 6.8$) compared with the original P_H value; (2) qualitative tests to determine the organic and inorganic acid radicals present; (3) ash analyses to determine the total base present; (4) studies of the reaction and titration values of malic acid salts, and such mixtures of them as appear likely to occur in the plant. The data are most complete for the juices of *Rochea falcata*, *Cotyledon obvallata*, and *C. linguaefolia*. The conclusion is reached that in these plants, and probably in all succulents, the concentration of hydrogen ions is determined by the relation between the quantities of acid and normal malate present.

On the alkaline side of the litmus end point the data may be grouped as follows: (1) titration from the litmus end point to that of phenolphthalein (P_H = about 9.2); (2) determination of nitrogen and in some cases phosphorus; (3) titration experiments with aluminum malate; (4) titration experiments with unknown and variable substances precipitated at the phenolphthalein point. It is concluded that aluminum malate and the unknown substances mentioned are the principal buffers in this region. The nitrogen and phosphorous compounds have very little effect. The titration to the phenolphthalein end point is admitted to be very unreliable. It seems unfortunate that as considerable quantities of the juice were available the electrometric method of titration was not used. Such results would have contributed much to the completeness and accuracy of the data.—THOMAS G. PHILLIPS.

Mutationists and selectionists.—JENNINGS[8] has attempted to reconcile the views of the "mutationists" and the "selectionists." The latter, headed by CASTLE, have claimed that selection can modify unit characters, and have presented striking evidence on the point. The mutationists have then demonstrated that these data may also be interpreted by assuming that there is but

[7] CROCKER, WM., Rev. BOT. GAZ. **64**:526–527. 1917.

[8] JENNINGS, H. S., Modifying factors and multiple allelomorphs in relation to the results of selection. Amer. Nat. **51**:301–306. 1917.

———, Observed changes in hereditary characters in relation to evolution. Jour. Wash. Acad. Sci. **7**:281–301. 1917.

one basic invariable unit determining the presence or absence of a character, plus numerous modifying factors; the number of the latter present in a given case determines the degree of expression of the character. The author admits that such modifying factors have been demonstrated in *Drosophila*, but goes on to show how "the objections raised by the mutationists to gradual change through selection are breaking down as a result of the thoroughness of the mutationists' own studies." For in *Drosophila* there have gradually been discovered not only 7 modifying factors for eye color, located on different regions of chromatin from the basic factor for eye color, but also 7 grades of the basic factor itself, that is, different conditions of the same unit. "What more does the selectionist want? Is not the controversy at an end?"

There still remains, however, a fundamental difference between the two views. The selectionists claim that these changes (in unit characters) are continuous, and in a definite direction determined by the standard of selection. The mutationists, on the contrary, claim that these changes occur in distinct steps (mutations), and do not occur in any definite order or direction as the result of selection. JENNINGS takes exception to this last claim of the mutationists, and presents some of his work on protozoa, to show the effectiveness of selection in a series of asexual generations.

There is much to be desired in such a reconciliation between the two schools, but more evidence must come in before there can be much hope of bringing it about. At present the views of the mutationists seem to be in better favor, chiefly because they give a much more definite basis for description of the phenomena of inheritance. "If one creates a hypothetical unit by which to describe phenomena and this unit varies, he really has no basis for description (EAST)."—MERLE C. COULTER.

Narcotic plants and stimulants.—SAFFORD[9] has published a very instructive account of plants used by the "ancient Americans" as sources of narcotics and stimulants long before the discovery of America. He indicates 13 such plants as chiefly in use, among them *Nicotiana*, *Datura Stramonium* (a source of atropine), *Erythroxylon Coca* (a source of cocaine). Other plants of minor importance are also noted. In concluding the summary, the following statement is made: "In view of the shortage of medicinal alkaloids resulting from the present war, it is suggested that investigations be made to determine the nature of the properties of these less-known narcotics, with a view to their utilization as substitutes for others now recognized in the standard pharmacopoeias."—J .M. C.

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[9] SAFFORD, W. E., Narcotic plants and stimulants of the ancient Americans. Smithson. Rep. 1916. pp. 387–424. *pls. 17*. 1917.